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Process_Based Management of Downy Brome in Salt Desert Shrublands: Assessing Pre- and Post-Rehabilitation Soil and Vegetation Attributes

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PROCESS-BASED MANAGEMENT OF DOWNY BROME IN SALT DESERT SHRUBLANDS: ASSESSING PRE- AND POST- REHABILITATION SOIL AND VEGETATION ATTRIBUTES

by

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Approved:

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ABSTRACT

As an ecosystem driver, downy brome (*Bromus tectorum* L.) presents obstacles to land rehabilitation efforts, including restoring desirable species cover. Because damaged ecosystems may have crossed both abiotic and biotic thresholds, ecologically-based control strategies may assist with altering successional trajectories and restoring desirable plant species. My thesis research had three objectives: 1) assess soil and vegetation relationships in degraded salt desert ecosystems prior to implementing downy brome control treatments, 2) determine the effects of control treatments on soil properties and resident plant species, and 3) evaluate the relative importance of shrubland soil type, herbicide type, and herbicide rate on seedling germination, growth, and establishment of perennial grasses and downy brome in a greenhouse experiment.

Two salt desert shrubland sites in Box Elder County, Utah were chosen for objectives 1 and 2. Objective 1 evaluated the relationships between downy brome, soil water, water infiltration, pH, electrical conductivity, sand, nitrate, phosphate, potassium, and magnesium using principal components analysis (PCA), factor analysis, and Pearson product-moment correlation coefficients. Objective 2 determined the effects of burning, herbicide, and mowing on downy brome, litter, bare ground, soil water, nitrate, carbon, phosphate, and magnesium using analysis of variance (ANOVA) and Wilcoxon sign rank tests. Objective 3 evaluated the effects of rimsulfuron and imazapic on emergence and growth of downy brome and two revegetation grass species using ANOVA.

For objective 1, I observed negative correlations between downy brome abundance and soil nitrate and water content which suggests that downy brome abundance is significantly impacting the content of these two soil properties. Objective 2

data indicate that control treatments significantly impacted downy brome abundance, soil resource availability, and resource fluctuation, which implies that downy brome can be reduced by control treatments, that its control can increase the availability of soil resources like nitrate and water, and can stabilize soil resource fluctuations. The results for objective 3 illustrate the importance of shrubland soil properties when using herbicides to reduce annual grasses and show that organic matter content and pH can significantly impact the relative performance of herbicides. Collectively this research helps identify the impacts on soil properties when using process-based management practices that reduce downy brome abundance.

(148 pages)

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CHAPTER 1

INTRODUCTION

Ecosystem processes within Great Basin shrublands have been altered by the persistent effects of past land-use and subsequent invasion of exotic annual plant species (West 1983a,b; Blaisdell and Holmgren 1984; Anderson and Inouye 2001; West et al. 2005). The invasive annual grass downy brome (*Bromus tectorum* L.) is the most notable invasive species in this region. Downy brome dominance is known to alter key ecological processes including disturbance regimes, soil nutrient cycling, community assembly, and successional pathways (Belnap et al. 2003; Rimer and Evans 2006; Adair et al. 2008). As an ecosystem driver, downy brome poses serious obstacles to ecosystem resilience and the ability of land managers to repair ecosystem structure and function (Belnap and Phillips 2001; Booth et al. 2003; Chambers et al. 2007).

Restoring shrublands to pre-disturbance conditions is not feasible because biotic and abiotic thresholds have been crossed (King and Hobbs 2006). A pragmatic alternative is to develop management goals to repair key ecosystem properties and processes, including ecosystem resilience (Whisenant 1999; Walker and Langridge 2002; Briske et al. 2008). The science of restoration ecology, and the application of ecological restoration to accelerate or initiate ecosystem recovery are rather new practices (Jordan et al. 1987), and the principles and tools to influence recovery are emerging for damaged Great Basin shrublands (Pickett et al. 1987; Sheley and Krueger-Mangold 2003; Krueger-Mangold et al. 2006; Sheley et al. 2009b). Collectively, these principles suggest that three critical

elements are needed: 1) assess the underlying above and belowground processes responsible for invasive plant dominance (Eviner and Chapin 2003; Eppstein and Molofsky 2007) 2) develop and apply effective management strategies that affect the causes of invasion and reduce invasive plant dominance (Krueger-Mangold et al. 2006; Sheley et al. 2009b) and 3) re-establish native and introduced plant species with appropriate traits to perform well in a restoration setting (Call and Roundy 1991; Jones et al. 2010). This process-based approach requires more than just controlling invasive species, but also actions that influence above and belowground ecological processes (Ehrenfeld 2003, 2004), directly remedy colonization dynamics (Adair et al. 2008), mediate interactions between invasive and desirable species (Eiswerth et al. 2009), and recognize the existence of potential plant-soil feedbacks (Ehrenfeld et al. 2005). A primary challenge facing rangeland management today is to integrate these elements.

Literature Review

Assessing Site Processes

Site assessment seeks to identify a broad array of potentially important ecosystem processes and predict which are likely responsible for continued dominance by invasive plants. These fall into three primary categories, including processes that regulate colonization, i.e., *site availability*, the relative abundance of different species, i.e., *species availability*, and the interactions of plants with their above and belowground environment, i.e., *species performance* (Pickett et al. 1987). Site assessment is a necessary exercise because it reveals how ecological processes

are influenced by historical events and the current ecological conditions, and how they can be modified to attain desired ecosystem trajectories and targets (Sheley and Krueger-Mangold 2003; King and Hobbs 2006). Below, I briefly review these three primary categories in reference to salt desert shrublands in the Great Basin.

Site availability. Historical disturbances are widely recognized as important drivers of invasive plant dominance in Great Basin shrublands. Since colonization by European immigrants in the 1840s, these ecosystems have been used for dryland farming and managed grazing systems, which broadly expanded in response to homesteading acts of 1862-1916 (Gates 1936). The dry farming boom was short-lived and unsustainable in the Great Basin because of the combined effects of low soil moisture and precipitation, changing climate conditions, and soil erosion (Stewart and Hull 1949). Consequently, this practice was largely abandoned, except where climatic conditions and soils matched the requirements of crop species, such as wheat and barley (Young and Evans 1989). Managing livestock grazing in these shrublands was also unsustainable, as native grasses and forbs had not evolved with heavy grazing pressure by domesticated ungulates (Mack and Thompson 1982). In addition, native vegetation could not possibly recover from stocking rates and grazing practices that were developed within mesic regions where immigrants had originated. Although grazing intensity has substantially declined in the last 50 years (Piemeisel 1951), the legacy of overgrazing and abandoned farming practices remain today (Jones 2000; Morris and Monaco 2010).

Theoretically, ecosystems that experience novel disturbances are believed to have crossed irreversible thresholds, and will remain in an altered ecosystem state, bounded by current climatic and edaphic conditions (King and Hobbs 2006; Suding and Hobbs 2009). Understanding and characterizing how these disturbances have altered site conditions and key ecosystem processes has been a major research thrust in the last 20 years (Allen-Diaz and Bartolome 1998; Elmore et al. 2006; Chambers et al. 2007). This research indicates that novel disturbances and altered ecosystem processes within Great Basin shrublands have reduced biological soil crusts, diminished the abundance of native herbaceous species, accelerated soil loss and erosion, and enabled broadscale colonization, spread, and dominance by exotic annual species, foremost among them, downy brome (Brandt and Rickard 1994; Young and Longland 1996; Young and Allen 1997; Muscha and Hild 2006).

Exotic annual plant dominance primarily influences site availability by maintaining a disturbance regime that makes it nearly impossible for native species to persist. When abundant, biomass produced by annual species creates a contiguous supply of fine fuel, i.e., litter, that increases the extent and intensity of fire (Young and Evans 1978; Young and Blank 1995; Brooks et al. 2004). Fire can kill certain shrub species with poorly protected meristems located above ground, including big sagebrush (*Artemisia tridentata* Nutt.) (Ziegenhagen and Miller 2009). In addition, perennial native grasses and forbs can be injured and experience reduced growth and seed production when fire return intervals are shortened (Wright and Klemmedson 1965; West 1994). On the contrary, annual grasses, which complete their life cycle

prior to the hot dry conditions when summer fires occur, are not directly hindered by fire, but their seeds can be diminished by fire, depending on fire dynamics (Sweet et al. 2008; Diamond et al. 2009). Consequently, the fires fueled by annual species favor their further dominance, and the subsequent decline in desirable species abundance (D'Antonio and Vitousek 1992; Brooks et al. 2004). Fires in Great Basin shrublands are believed to have become more frequent since European colonization, but this trend has not been fully quantified, and is often implied from historical patterns and indicators (Mensing et al. 2006). However, in salt desert ecosystems, fire has indeed emerged as a novel disturbance to these low elevation shrublands in the last 30 years (West 1994; Jessop and Anderson 2007; Haubensak et al. 2008).

Mechanistically, disturbance regimes alter site availability through their influence on niches and safe sites for plants and seed (Eckert et al. 1986; Lamont et al. 1993). For example, disturbance directly modifies competitive interactions (Eliason and Allen 1997); environmental conditions (Melgoza et al. 1990; Bradford and Lauenroth 2006), litter dynamics (Sheley et al. 2009b), seed movement (Chambers 2000), and resource supply rates (James and Richards 2007). Characterizing how disturbance influences these processes is thus an important aspect of clarifying how site availability can be modified by managers to yield a more desired plant community.

Species availability. Species availability and subsequent colonization depends on propagule dispersal and propagule pressure (Marlette and Anderson 1986; Rodríguezi-Gironés et al. 2003; Chytry et al. 2008). These mechanisms of colonization are critical components of succession because viable seeds must be

present through dispersal, from seed banks, or be introduced artificially, as in a rangeland seeding (Call and Roundy 1991; Cox and Anderson 2004). Recent theoretical discussions suggest that colonization dynamics follow certain assembly rules (Ackerly 2003), where both biotic and abiotic filters regulate propagule dispersal and propagule pressure (D'Antonio et al. 2001; Mazzola et al. 2008). In altered shrublands of the Great Basin where disturbances are frequent, colonization is dominated by exotic annual species, which produce abundant seed that dominate seed banks (Humphrey and Schupp 2001). For example, individual plants of downy brome can produce up to 6,000 seeds, most of which will germinate the following fall and rapidly recolonize after disturbance (Smith et al. 2008). In contrast, native perennial grass and shrub species have much slower growth rates and have lower seed output (Young and Evans 1978). Thus, remnant native species experience a highly competitive environment, with reduced fecundity and productivity caused by exotic annual species dominance, which allows exotics to persist even after earnest control efforts (Borman et al. 1991; Morris et al. 2009).

Assembly rules following disturbance also suggest that priority effects may be responsible for exotic annual species dominance (Tillman 1994; Corbin and D'Antonio 2004; Ludlow 2006). Priority effects describe how exotic annual species gain "priority" in colonization because they often have earlier phenological development, and are more represented in seed banks (Humphrey and Schupp 2001; Rice and Dyer 2001). For example, species that arrive and germinate first can gain dominance and control subsequent community pathways, i.e., successional

trajectories (Mack and D'Antonio 1998; Corbin and D'Antonio 2004). Priority effects must be removed or diminished before the performance of desirable perennial species can even be realized. These colonization and species availability obstacles suggest that management actions will need to systematically reduce propagule pressures of invasive species in unison with artificially seeding of desirable species and fostering their future dispersal (Corbin and D'Antonio 2004). Furthermore, assessing site conditions will provide critical information about colonization dynamics and indicate potential ways to manipulate species availability when developing a management plan.

Species performance. There is a robust scientific literature demonstrating functional differences between invasive species and the native species that are negatively impacted by their presence (Vitousek et al. 1997; Ehrenfeld 2003). However, because many factors and processes regulate species performance within an ecosystem, predicting why and which species will become invasive, and identifying which ecosystem will be invaded has been challenging (Reichard and Hamilton 1997; Moles et al. 2008). A few of the widely recognized factors important to regulating species performance include resource availability, and the ability of plants to capture resources, ecophysiological traits, plant response to stresses, and tradeoffs in life history traits (James et al. 2010).

The influence of resource availability on plant performance has long been recognized. However, formal theories that seek to explain how resource dynamics regulate relative species competitive ability, species diversity, ecosystem functions,

and exotic species invasion are relatively recent (Huenneke et al 1990; Grime et al. 1996; Goldberg and Novoplansky 1997; Davis et al. 2000). In general, temporal and spatial aspects of resource capture have emerged as critical components of explaining these processes. Annual exotic species perform better under elevated resources for many reasons, including the coincidence of their phenology and temporal resource availability in shrubland ecosystems (Blank 2008). Alternatively, native perennial species often initiate growth and resource capture after exotic species have pre-empted limiting resources (Melgoza et al. 1990; Chambers et al. 2007). Pre-emption is a consequence of exotic annual species having lower temperature thresholds for root growth (Bradford and Lauenroth 2006), higher nutrient and water uptake rates (Melgoza et al. 1990; Evans et al. 2001), and faster growth rates than native perennial grasses (Arredondo et al. 1998). Thus, without management intervention of ecological processes, invaded sites favor exotic annual species performing at their full biological potential, and their continued dominance.

High exotic annual species performance and dominance on Great Basin shublands may also be perpetuated by plant-soil feedbacks wherein soil nutrient cycling processes have been altered in ways that primarily benefit annual species (Ehrenfeld and Scott 2001; Evans et al. 2001; Norton et al. 2004; Blank 2008). For example, evidence suggests that downy brome-dominated patches have higher nitrogen mineralization rates, higher total nitrogen availability, abundant low C:N ratio leaf litter, and higher litter decomposition rates than adjacent patches dominated by native species (Evans et al. 2001; Booth et al. 2003; Norton et al. 2004; Rimer and

Evans 2006). Not only do these alterations favor downy brome, but they may promote soil organic matter decomposition and further impoverish sites, making them potentially more difficult to restore with native species (Norton et al. 2004).

Reducing the performance of exotic annual species requires carefully executed management efforts that effectively manipulate the processes responsible for their success while influencing processes that favor desirable species. For example, if site and species availability have been adequately remedied by reducing disturbance frequency and priority effects that favor annual species, the performance of desirable species can be enhanced to trigger different ecosystem assembly patterns where interference from exotic annual species is minimized. Achieving these conditions may be one of the most challenging aspects of land management in salt desert ecosystems dominated by downy brome.

Process-based management

Managing processes has not been the primary objective of land management in the past. For example rangeland managers in grazed systems historically adopted the notion that plant communities change linearly toward a climax endpoint dominated by certain late successional species (Clements 1936), and that managers could adjust livestock stocking rates to reverse successional trends (Dyksterhaus 1949). However, this interpretation could not predict non-linear dynamics, or indicate underlying mechanisms responsible for vegetation dynamics (Westoby et al. 1989; Briske et al. 2008). Thus, a successional model that incorporates the mechanisms and pathways of succession into a mechanistic framework for process-based management

was developed for predicting vegetation change and developing desired changes (Connell and Slatyer 1977; Pickett et al. 1987; Sheley et al. 1996; Sheley et al. 2010). This model has recently been shown to greatly increase restoration success over traditionally applied integrated weed management (Sheley et al. 2009a), and is gaining credence within rangeland and restoration ecology (Sheley and Denny 2006; Sheley et al. 2007; Sheley and Bates 2008; Sheley et al. 2008). This process-based approach to managing invasive plants advocates assessing site conditions, identifying the ecological processes in need of repair, applying appropriate tools, and re-assessing management outcomes (Fig. 1).

A primary challenge to process-based management is developing the appropriate methods and tools to go beyond treating symptoms of invasive plant problem and begin influencing processes that yield desirable change (Sheley and Krueger-Mangold 2003; Krueger-Mangold et al. 2006). In addition, the idea that influencing the underlying problem as opposed to 'killing the weed', is necessary (Sheley and Krueger-Mangold 2003). Although, many tools currently exist to remedy invasive annual grass infestations, there is a need for greater understanding of their ability to affect site availability, species availability, and species performance, and whether these tools effectively direct succession to a more desirable vegetative state. Assessing whether potential tools influence the intended ecological processes and yield the desired outcomes is thus necessary to develop predictive, process-based management strategies. Below, a few of the most contemporary management tools

are reviewed, and their merits are briefly discussed in terms of the processes that they are intended to modify.

Prescribed fire. Prescribed fire is an integral tool of ecosystem management that directly modifies all three causes of succession. Fire directly modifies site availability by removing residual annual invasive plant litter and improving seedbed conditions for seeded species establishment (DiTomaso et al. 2006; Blank et al. 2007; Allen et al. 2008). In addition, fire can alter species availability by inhibiting invasive plant propagule pools, seed viability, and their dispersal when standing dead and residual litter of is consumed by burning (Vermeire and Rinella 2009). Fire is most effective when applied after plants have flowered, yet seeds have not matured, or fallen to the ground (i.e., purple stage) (Evans and Young 1978). When prescribed fire is applied at purple stage, fire interferes with the life strategy of undesirable species, thereby modifying species performance. Collectively, fire can adequately prepare sites for the seeding and successful establishment of desirable species.

The effectiveness of fire at influencing the causes of succession depends on fire intensity (Wrobleski and Kauffmann 2003; Brooks et al. 2004), which is determined by several ecosystem properties, including fuel load and fuel flammability (Brooks et al. 2004). When fire intensity is low, fires may create patchy fire distribution that does not thoroughly burn litter or residual undesirable seed banks, which could allow annual grass dominance to return to pre-fire levels (Wrobleski and Kauffmann 2003). Alternatively, when fire intensity is too high, it can potentially volatilize soil nutrients from soils and organic matter (Rau et al. 2007, 2008). Fire-

mediated nutrient loss may negatively influence germination, emergence, and establishment of desirable seeded perennial species in the following spring during critical establishment periods, even though soil N and C may return to pre-fire levels over the long term, (Rau et al. 2009). These observations suggest that moderate fire intensity, which is most likely to occur in the late fall or early spring when perennial grasses have either matured or are still quiescent, respectfully, may ideally influence residual litter and seed banks and result in desirable modifications in plant communities dominated by invasive annual grasses (Brooks et al. 2004).

Mowing. Mowing is a disturbance, similar to targeted grazing, that can be used to primarily influence species availability and performance by directly reducing standing biomass and reproduction via direct effects on seed production of exotic annual grasses (Hempy-Mayer and Pyke 2007). For example, if mowing is applied when invasive annual grasses have initiated flowering, yet seeds are not mature (i.e., boot stage), then seed dispersal can be effectively reduced (Eliason and Allen 1997; Cox and Allen 2008). Mowing also impacts species performance because biomass removal can serve as a stress factor to shift competitive balances between exotic annual grasses and desired species (Hempy-Mayer and Pyke 2007; Cox and Allen 2008; Diamond et al. 2009). Furthermore, site availability may also be affected with mowing applications by altering disturbance regimes. For example, removing the abundant standing biomass and litter produced by annual grasses can reduce the fine fuels that carry wildfires in Great Basin shrub ecosystems (Haferkamp and Karl 1999; Hempy-Mayer and Pyke 2007). Although mowing is useful at reducing standing

biomass, litter, seed production, and potential dispersal, applications in shrubland ecosystems will be limited to shrublands dominated by annual grasses, where mowing will not damage shrub species. Mowing may also not adequately eliminate residual seed banks (Cox and Allen 2008) and poor control of residual seed banks increases the potential for undesirable species to reestablish and continue their cycle of dominance, because downy brome seeds can stay viable for 2 to 5 years once they have dispersed onto the soil surface (Smith et al. 2008). These limitations suggest that mowing will be more feasible where desirable shrubs are not present, or in regions where the benefits of mowing will simultaneously reduce the abundance of less desirable shrub species and invasive grass.

Pre-emergence herbicides. Inhibition of fast-growing annual grasses is possible with pre-emergence herbicides because they are typically designed to reduce weed abundance, seed production, and subsequent litter production. In particular, pre-emergence herbicides that target the production of acetolactate synthase (ALS), a key enzyme responsible for branched amino acid production (valine, leucine, and isoleucine), may be used to directly reduce germination and/or seedling growth of invasive annual grasses (Lair and Redente 2004). Preventing germination of annual grasses limits their potential colonization and dispersal, and reduces overall production capacity (Monaco et al. 2005; Chambers et al. 2007; Cox and Allen 2008). Collectively, this tool has shown considerable promise for short-term control of annual grasses, but field studies have unfortunately produced variable success, and invasive annual grasses often rebound to pre-treatment abundance levels.

Understanding the sources of poor success, or alternatively, the factors associated with good success will yield improved land management.

Effectiveness of pre-emergence herbicides has been variable (Krueger-Mangold and Sheley 2003; Monaco et al. 2005; Kyser et al. 2007; Sheley et al. 2007), and may depend upon herbicide type, herbicide rate, non-target species injury, and interactions with site characteristics, including soil properties and climate (Shinn and Thill 2004; Monaco et al. 2005; Kyser et al. 2007; Morris et al. 2009). While pre-emergence herbicides have been shown to significantly reduce annual grass cover and density for both downy brome and medusahead (*Taeneatherum caput-medusea* (L.) Nevski) on annual dominated Great Basin salt desert shrublands, populations often return to pre-treatment levels within a few years because seed banks are not sufficiently reduced or non-target species are significantly injured and fail to produce anticipated competitive influences on annual grasses (Monaco et al. 2005; Davison and Smith 2007; Kyser et al. 2007; Sheley et al. 2007). Non-target herbicide injury suggests that identifying the optimal herbicide application timing and rate, and which species can be safely seeded to avoid herbicide injury should be a research emphasis (Shinn and Thill 2004; Kyser et al. 2007; Baker et al. 2009). Quantification of these variables could further help identify the factors responsible for variable results, and whether applications will yield success or failure in Great Basin shrublands.

Integrated process-based management approach

Process-based management is intended to manage invasive species through targeting the causes of succession. While independent applications of fire, mowing, and herbicide potentially impact causes of succession, no tool alone adequately impacts all causes of succession simultaneously. Therefore, it may be more prudent to use these tools in combinations in order to realize the maximum effects. Research that evaluates the combined influence of fire, mowing, and pre-emergence herbicides in the Great Basin is currently limited, especially in for salt desert shrublands. Quantifying how these integrated tools impact the ecological processes that effect plant community change could help clarify ecological principles, and define improved strategies for annual grass invaded ecosystems in the Great Basin.

Research Objectives

The overarching goal of my research is to assess and evaluate this process-based approach in salt desert shrublands that have experienced long-term degradation and invasion by downy brome. Specifically, my objectives are: 1) Assess soil and vegetation relationships in a degraded salt desert ecosystem prior to implementing a process-based management approach; 2) Determine the effects of process-based management tools (i.e., prescribed fire, mowing, and pre-emergence herbicide) on key soil properties; and 3) Evaluate the relative importance of shrubland soil type, herbicide type, and herbicide rate on seed germination, seedling growth, and seedling establishment of perennial grasses and downy brome in a controlled greenhouse experiment. I anticipate that my thesis research will help integrate the elements of

process-based invasive plant management and generate insights into its application within salt desert shrublands of the Great Basin.

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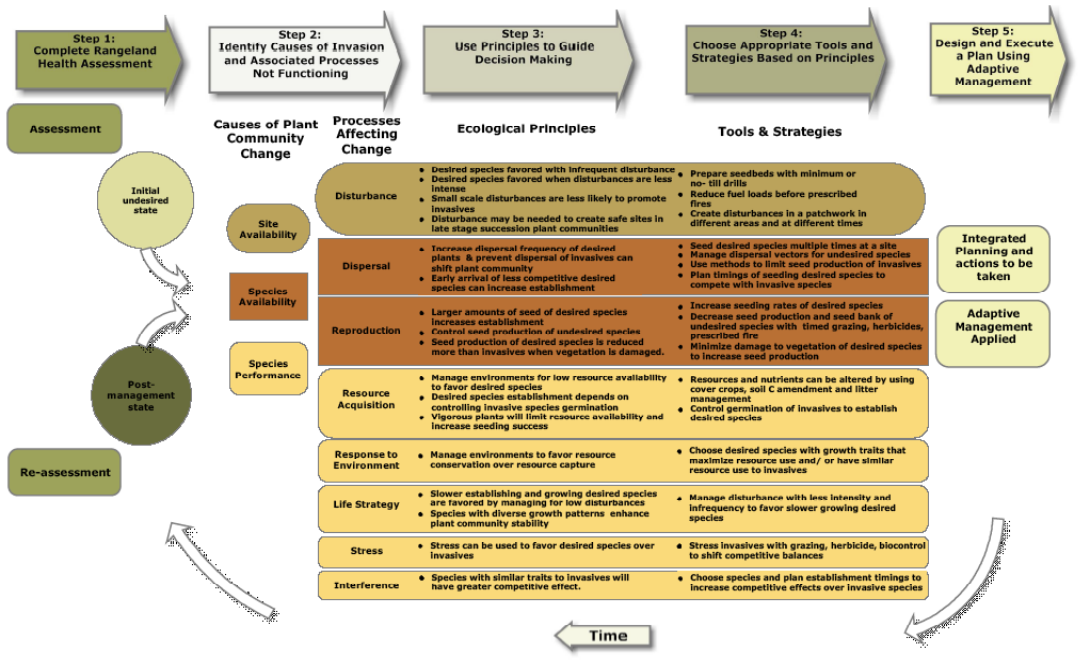

Figure 1: Process-based (ecologically based invasive plant) management model

CHAPTER 2

INFLUENCE OF ANNUAL GRASS CONTROL TREATMENTS ON PLANT-SOIL RELATIONSHIPS IN SALT DESERT SHRUBLANDS

Abstract

Understanding the plant-soil relationships of downy brome invasion (*Bromus tectorum* L.) within salt desert shrublands of the Great Basin is a precursor to developing effective management strategies. I measured vegetation and ground cover, gravimetric water content, water infiltration, soil texture, pH, electrical conductivity (EC), and exchangeable soil ions (NO_3-N, Mg^{2+}, K^+, and PO_4^-) at two salt desert shrubland sites in northwestern Utah before and after implementing the independent and combined downy brome control treatments of prescribed fire, pre-emergence imazapic herbicide, and mowing. Analysis of pre-treatment data with principal components analysis (PCA) and common factor analysis revealed that downy brome cover was oppositely correlated with soil water and NO_3-N along a primary PCA axis. Analysis of pre- and post-treatment data using analysis of variance to test the independent and combined effects of burning, herbicide application, mowing indicated that burning and herbicide treatments significantly ($P < 0.1$) reduced downy brome and litter cover and increased soil nitrate accumulation, soil water content, and bare ground cover. Burning and herbicide application also significantly ($P < 0.1$) reduced interannual fluctuation in downy brome cover, soil water content, and nitrate accumulation relative to untreated areas.. Analysis of resident species cover data with

Wilcoxon sign rank tests to contrast pre- and post-treatment within each of the eight treatment combinations indicated that nearly all treatment combinations that included burning prevented significant increases in Russian thistle cover at one site, while squirreltail cover at the other site significantly increased in all treatments that included burning. Results suggest that downy brome strongly influences critical soil resources within these salt desert shrublands, and that control treatments designed to reduce downy brome abundance simultaneously impact soil resource availability and fluctuation, as well as influence the composition and abundance of resident species by reducing propagule pools and impacting soil surface characteristics.

Introduction

Invasive plant species pose a major threat to rangeland ecosystems and complicate managerial efforts to improve wildlife habitat, forage productivity, and reduce wildfire risk. After initial colonization and spread of invasive plants, their impact and dominance may increase with time, depending on their functional distinctiveness within the ecosystem (Mack et al. 2000; Strayer et al. 2006). At this point, ecosystem processes are largely controlled by the invasive species (MacDougal and Turkington 2005), including plant-soil resource dynamics and disturbance regimes (D'Antonio and Vitousek 1992; Ehrenfeld et al. 2005). Moreover, when these processes are primarily driven by invasive species, in the absence of functionally diverse perennial species, a perpetual feedback cycle is developed wherein successional dynamics are modified (Kulmatiski et al. 2008; Beckage et al.

2009). Consequently, there is great need to understand plant-soil relationships of invasive-plant-impacted ecosystems and explore how rehabilitation actions influence these relationships.

The species composition of plant communities strongly impacts soil resource availability (Wedin and Tilman 1990; Tilman 1999). In particular, reductions in functional diversity, a measure of the range of species traits in a species pool, leads to underutilized soil resources, making ecosystems more susceptible to invasion and dominance by non-native plants species (Davis et al. 2000; Symstad 2000; Fargione et al. 2003). When functional diversity is lost, soil resources are underutilized because rates of acquisition by invasive species are lower relative to when native species are present (Dyer and Rice 1999; Funk et al. 2008; Drenovsky et al. 2008). Altered resource availability also may stem from soils dominated by invasive species having higher rates of litter decomposition, nitrogen mineralization, and nitrification than soils associated with displaced native species (Ashton et al. 2005; Chapman et al. 2006; Liao et al 2008; Van der Putten et al. 2009). In addition to altered resource availability, invasive species dominance may exacerbate fluctuations in resource availability that can occur from year to year, or within a year (Chambers et al. 2007). These fluctuations are a result of invasive species differing fundamentally from resident native species in life history traits, including phenological development, primary productivity, and seasonal soil resource acquisition (Maron and Jefferies 1999; Evans et al. 2001; Ehrenfeld 2003). For example, a pronounced pulse of soil nitrogen availability occurs in the autumn following senescence of an invasive annual

grass that is not present where perennial grasses remain dominant in cold deserts of the Great Basin in North America (Booth et al. 2003; Hooker et al. 2008).

Annual plant species invasions are predicted to exacerbate, possibly irreversibly, the effects of variable precipitation and droughts on species composition and growth within semiarid ecosystems (Schwinning et al. 2005). Although interannual variability in productivity and soil resources is strongly correlated with annual precipitation (Knapp and Smith 2001), and is inherent in annual-plant-dominated ecosystems (Bradley and Mustard 2005; Chambers et al. 2007), it poses a particular challenge to restoring perennial species composition. For example, biomass production can vary on annual plant-dominated shrublands between 5 and 10-fold depending on precipitation (Hull and Pechanec 1947; Stewart and Hull 1949; Uresk et al. 1979), which occurs in both the fall and spring, over a very short period (Stewart and Hull 1949; Morrow and Stahlman 1984). Thus, downy brome is still likely to dominate and persist in unfavorable precipitation years because it produces enough seeds to re-establish from seed banks (Stewart and Hull 1949; Young and Evans 1978; Humphey and Schupp 2001; Smith et al. 2008). High interannual variability in productivity and seed production, coupled with frequent disturbance, and altered plant-soil-microbial dynamics (Kuske et al. 2002; Hawkes et al. 2005, 2006), make annual-plant-dominated systems considerably unstable, perpetuating a degraded vegetation state characterized by cyclic succession between annual species (Piemeisel 1951; Allen and Knight 1984; Prevéy et al. 2010). For example, wildfire risk is and frequency is greatly increased when downy brome litter becomes abundant in

shrublands (D'Antonio and Vitousek 1992). Following fire, soils are typically bare, which favors the germination of annual forbs such as tall tumble mustard (*Sisymbrium altissimum* L.), western tansy mustard (*Descurainia pinnata* [Walter] Britton), and Russian thistle (*Salsola kali* L.) (Piemeisel 1951; Young and Evans 1975). The litter produced by annual forbs then facilitates the establishment of downy brome, which typically does not germinate on bare soil (Piemeisel 1951), but requires higher soil moisture and less variable temperature created by a litter layer (Evans and Young 1984; Facelli and Pickett 1991). For this reason, efforts to control invasive annual grasses often target seed and biomass production, and litter accumulation to minimize recolonization potential, resource competition and interference on emerging revegetation species, and wildfire frequency (DiTomaso et al. 2010; Pyke et al. 2010). Although these control treatments are very costly, they are employed to create a window of opportunity wherein perennial species can be reintroduced back into the system and potentially trigger a more favorable ecosystem successional pathway. When control treatments are unsuccessful, ecosystems may remain in a degraded, unstable state; however, when control treatments are successful, they may simultaneously decrease annual species abundance while facilitating the performance of residual species.

In addition to impacting invasive annual grass abundance, control treatments also profoundly influence soil resource availability and other soil physiochemical properties. The primary treatments used to control invasive annual grasses at management-level scales include prescribed fire, pre-emergence herbicide

application, biomass removal, and revegetation (DiTomaso et al. 2010; Pyke et al. 2010). Prescribed fire is commonly used to consume seeds of invasive species, and reduce the accumulation of litter that aids annual grass establishment, obstructs herbicide contact with soil, and elevates wildfire risk (DiTomaso et al. 2006; Sweet et al. 2008). The effects of prescribed fire on vegetation and soils depend on fire intensity and severity (Neary et al. 1999). In general, soil water and mineral nutrients will increase as their utilization by fire-damaged plants is reduced, and because when litter is volatilized during combustion, extractable concentrations of key minerals, including nitrate and phosphate, can be elevated for up to three years (Rau et al. 2007). Soil heating may also affect water repellency of the soil surface and water infiltration (DeBano 2000; Rau et al. 2005). Annual plant seedling emergence and abundance can also be reduced with soil-active pre-emergence herbicide applications. Imazapic (Plateau ®) is a pre-emergence herbicide that is used in restoration projects throughout the west and has an average persistence in soil of about 120 d (Vencill 2002; Kyser et al. 2007; Davies 2010). Coincidently, pre-emergence herbicide applications can increase the accumulation and availability of mineral nitrogen by reducing the abundance of emerging annual grass seedlings, which are a major sink for soil nitrogen in the early autumn (Booth et al. 2003; Flory and Clay 2009). In addition, residual herbicide bioavailability may also injure non-target perennial species (Obrigawitch et al. 1998; Hollaway et al. 2006), as well as impact plant utilization of nutrients until herbicide bioavailability is dissipated (Wilson et al. 2010). Similar to fire and herbicides, livestock grazing, mowing, or general biomass

removal, can be used to effectively reduce annual grass seed production, litter accumulation, and annual-grass interference on the performance of residual perennial species (Wilson and Clark 2001; Seabloom et al. 2003a; MacDougal and Turkington 2005; DiTomaso et al. 2008). For example, Maron and Jefferies (2001) show that when mowing was used to suppress annual species and shift plant community dominance to residual perennial species, less soil nitrogen was leached from fallow annual plant control plots in late fall and winter, and substantially greater amounts of nitrogen was retained in mowed plots, due to the presence of perennial plants possessing large amounts of belowground biomass in early spring. Similarly, Prober and Lunt (2009) show that establishing desirable perennial species via revegetation can reduce soil nitrogen availability and maintain low mineral N concentrations over time by the production relatively recalcitrant, high C:N litter that slows nitrogen cycling and increases nitrogen immobilization (Hobbie 1992; Aerts and Chapin 2000).

Because the control treatments reviewed above are capable of simultaneously influencing critical aspects of annual grasses growth and soil resources, the capacity to influence an underlying mechanism for annual grass persistence--underutilized resources that fluctuate--could be within the reach of land managers. Consequently, characterizing how these common control treatments simultaneously reduce the abundance of annual weed species, impact soil resource availability and season fluctuations, and initiate desirable successional trajectories will help refine ecologically-based invasive plant management strategies (Sheley et al. 2010). Such

research may also clarify the mechanisms responsible for invasive annual plant persistence and the associated difficulty in facilitating the re-colonization and establishment of desirable plant species, which is currently needed for semiarid grasslands, shrub steppe, and shrubland ecosystems of western North America (Eviner et al. 2006; Chambers and Wisdom 2009; Prevéy et al. 2010). To assist in this effort, I designed a field experiment to evaluate three specific objectives and their associated predictions. For my first objective I sought to characterize the relationships between soil properties and the abundance of downy brome (*Bromus tectorum* L.) in two highly disturbed salt desert shrubland sites in the northeastern Great Basin. The associated prediction is that within sites, sampling plots will have a high degree of variability, which is explainable by the abundance of downy brome and its influence on soil resource availability. My second objective sought to evaluate how the independent and combined control treatments of prescribed burning, pre-emergence herbicide application, and targeted biomass removal influence downy brome abundance the availability and fluctuation of soil nutrients. Accordingly, I predict that control treatments, implemented to reduce downy brome, will increase overall soil nitrate and water availability, yet decrease interannual variation in downy brome abundance and soil resource availability. My third objective sought to determine the influence of control treatments on the abundance of resident perennial species and the annual species whose successional dynamics are closely coupled with downy brome. My associated prediction is the that the abundance of all species will generally increase where downy brome abundance is reduced, but that annual species

abundance will also depend on the unique ways that control treatments impact the accumulation of litter on the soil surface. Addressing these predictions at operational scales will aid in developing improved management practices for annual-grass-invaded ecosystems. In addition, this research will clarify the theoretical understandings of relationships between exotic annual grass abundance and soil resource availability/fluctuation.

Materials and Methods

Study location and description

Two salt desert shrubland sites, located 5 km south of Park Valley, Utah (Zone 12 N), were chosen for our study. Sites were 50 ha (Upper site) and 100 ha (Lower site), 1 km apart, with a lower site closer to the northern tip of the Great Salt Lake (309821 m E, 4627117 m N) and an upper site located to the northwest (311386 m E, 4625481 m N). Ecological Site classification is semi-desert alkali loam (black greasewood) (NRCS 2010). Soils are in the Kunzler-Lembos series and are classified as coarse-loamy, mixed superactive, mesic durinodic xeric haplocalcids and coarse-loamy, mixed, superactive, mesic xeric argidurids. Parent material is derived from alluvium, which has been deposited from the canyons of the Raft River Mountains to the north. Climate is characterized by cold snowy winters and hot dry summers, with most of the moisture occurring through snow melt and spring rains. Precipitation ranges from 200-300 mm per year with mean annual precipitation of 275 mm and mean annual air temperature of 10 °C.

In the absence of soil disturbance, vegetation is typically dominated by shrubs; namely, black greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), Wyoming big sagebrush (*Artemisia tridentata ssp. wyomingensis* [Beetle & Young] S.L. Welsh), and rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird ssp. consimilis [Greene] G.L. Nesom & Baird). Furthermore, the herbaceous understory is composed of Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth) and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey). However, this site has experienced recurring problems with frequent wildfire and exotic annual plant invasions in the past 30 years. For example, a large wildfire burned this region in 1983, which provided suitable conditions for invasive annual species expansion, and subsequent fires in 1999 and 2004. Consequently this region and both research sites were dominated by exotic annual species including: downy brome (*Bromus tectorum* L.), halogeton (*Halogeton glomeratus* [M. Bieb.] C.A. Mey.), *tumble mustard* (*Sisymbrium altissimum* L.), and Russian thistle (*Salsola kali* L.) in 2008. Following the 2004 wildfire, the upper site was seeded with crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), but the seeding was deemed unsuccessful, even though it did establish patchily in areas. Overall, the two research sites represent ‘poor condition’ semi-desert alkali loam (black greasewood).

Experimental design

Two replicate locations at each research site were divided into eight units with comparable proportional dominance by downy brome, yet of different size, ranging from 25 to 63 ha. Planned downy brome control treatments were assigned to the eight

units using a split-plot design (Fig. 2). Within each unit, a total of 14 sampling points with visually consistent vegetation cover and density were established in March 2009. Sampling points consisted of a 3.5 x 3.5 m plot.

Prescribed burns (whole-plot factor) were conducted on 4 November 2009 by igniting the perimeter of units with propane or drip torches, and allowing the prevailing wind to carry the fire. The fire was contained within the appropriate units by installing fire lines (100-m wide) one week before the burning. Immediately behind the burning front, an 8-person burning crew ignited patches that failed to burn, paying close attention to burn the previously established sampling plots. Weather conditions on the day of burning were an average of 6.9 ºC with a high of 17.3 ºC and low of -0.5 ºC, wind speed was 8.7 KPH (ESE), and relative humidity was 75%. Given these conditions of this autumn fire, it was estimated that only 75% burned of units burned.

The pre-emergence herbicide imazapic (split-plot factor) was applied aerially with piper PA-36 Pawnee Brave agricultural aircraft with a 15 m boom on 18 November 2009. Herbicide was applied at the rate of 78 g ai/ha carried in 22 L water/ha sprayed at 7.6 m above the surface at 160 km/hr. Weather conditions on the day of herbicide application were an average of 1.6 ºC with a high of 8.3 ºC and low of -5 ºC, wind speed was 17.7 KPH (WSW), and relative humidity was 53 %. The first measurable precipitation event following application was on 21 November 2009.

The 14 plots in each unit were randomly assigned to a mowing treatment that was applied on 25 June 2009 using a 60 cm diameter push mower. Plots were mowed

Mowing at a height of 5 cm the target plant, downy brome, was at boot stage or when 10% of all downy brome plants reach reproductive stage.

Sampling approach

At each sampling plot soils, plant cover and plant density of all encountered species was inventoried in prior- and post-downy brome control treatments in May of 2009 and 2010, respectively. Within a plot, vegetation and soil were sampled at four fixed locations within the center 2 m^2 of each plot by placing a 20 x 50 cm Daubenmire frame on the soil surface and estimating percentage cover for each species encountered in the frame (Herrick et al. 2005). Soils were collected using a 10 cm diameter x 20 cm length corer, aggregated and mixed, and kept in a chilled cooler during transport to the laboratory. Soil hydraulic conductivity (HC) was measured once in April 2009 adjacent to the soil sampling locations using mini-disk infiltrometers (Mini-disk infiltrometers, Decagon Devices, Pullman, WA). Infiltrometers were filled with water, placed on bare soil, and the loss of water was measured every 30 s for 2 min to determine the infiltration rate (cm s^{-1}). Soil minerals were measured in both 2009 and 2010 using sets of ion exchange membrane probe (PRS^{TM} probes, Western Ag Innovations, Saskatoon, SK, Canada). A probe set consisted of anion and cation resin stakes, which were inserted into the moist soil in late April where HC measurements were taken. Probes were retrieved after 60 d. In brief, the 10-cm^2 resin captures ions that move through the soil solution. After retrieval from the field, probes were washed in deionized water and sent back to the

manufacturer for analysis of nitrate (NO_3-N) calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+), and phosphate (PO_4^-) (Drohan 2005).

Field-collected soil was used to determine gravimetric water content by taking a 30 g sample from each plot, and drying it in a convective oven at 100 °C and reweighing (Topp 2002). The field-collected soil samples were air-dried for 14 d and passed through a 2 mm sieve to further remove debris and gravel. Soil texture was determined using the hydrometer method to quantify percentage sand, silt, and clay (Gee and Bauder 1986). A 40-g sample was mixed with 100 mL of a sodium hexametaphosphate-water solution and 250 mL of deionized water, shaken at 150 rpm for 1 h, placed into a cylinder, and the cylinder was filled with deionized water to attain 1 L. A custom plunger was used to mix the slurry before measuring its temperature and density (g L^{-1}) after 30 s and 1440 min with a bouyoucos hydrometer (14-331-5C, Thermo Scientific, Beverly MA). Soil pH was measured by mixing a 15-g soil sample with 30 mL of deionized water, shaking at 100 rpm for 30 min, then measuring the slurry with a pH meter (Orion 3 star bench-top pH meter, Thermo Scientific, Beverly, MA) (Thomas 1996). Electrical conductivity was determined on 50 g of soil mixed with 50 mL of deionized water, shaken at 200 rpm for 2 hrs, and filtered through a filter paper (Grade 4, Whatman International Ltd., Maidstone, England) using a vacuum system. Electrical conductivity was measured on the filtered solution with an ionic probe (Orion 3 star bench-top conductivity meter, Thermo Scientific, Beverly, MA) (Rhodes 1996).

Statistical analyses

The distribution and homogeneity of variances for the measured variables was assessed, and each variable was subjected to transformations to improve normality as needed. Although most data were normal for 2009 and 2010, there were a few transformations that were made during these years. Transformations on data collected in 2009 are as follows; a log transformation was used for water infiltration, electrical conductivity, and nitrate. In addition, a log +1 transformation was performed on cover of downy brome, bare ground, and litter. Data collected in 2010 that were subjected to transformations included a square root transformation for downy brome cover and log +1 transformation for bare ground, and nitrate.

To address objective 1, the measured soil and vegetation variables from 2009 were first standardized with a transformation so that the mean equals 0 and the variance equals 1. Variables were then analyzed with principal components analysis (PCA) and common factor analysis to evaluate the relationships among variables using JMP 8.02 (SAS Institute Inc. Cary, NC). For simplicity of interpretation, we extracted only the first two principal components because our intention was to explain the variation of this ecosystem using two-axis bi-plots. Subjecting the two extracted PCA components to a Varimax rotation generated uncorrelated, orthogonal, high factor loadings for the most important variables. Factor loadings were graphed as x,y-plots, which illustrate the correlation between each variables and the two extracted PCA axes. In addition, the association between downy brome cover, two PCA-axes, and the soil variables from measured 2009 was determined with Pearson product-moment correlation coefficients. All analyses were performed using JMP 8.02 (SAS

Institute Inc., Cary NC). Associations with significance greater than $P < 0.05$ are indicated on graphs. Further evaluation was done on the relationship between downy brome and electrical conductivity at the lower research site. This relationship is graphed using Microsoft Excel 2007 © and presented with the logarithmic trend line.

Objective 2 was evaluated using PROC Mixed ANOVA in SAS (SAS Institute Inc., Cary, NC). Treatments included the independent and combined factors of burning, herbicide application, mowing, and year. The model analyzed treatment impacts on plant and soil variables using a split-plot design with factorial treatment arrangements and census year as a dependent random factor. Variables included downy brome cover, litter cover, bare ground cover, soil water content, and soil nitrate. Sites were analyzed separately because they differed in downy brome cover, soil texture, and elevation; the upper site had a higher elevation, higher clay and silt content, and lower downy brome cover (Table 2).

Objective 3 was addressed by using Wilcoxon rank sums tests, performed in JMP 8.02 (SAS Institute Inc., Cary NC), to independently compare resident species cover between 2009 and 2010 within the eight treatment combinations. Plant species evaluated included three non-native annual forbs; bur buttercup (*Ranunculus testiculatus* Crantz), Russian thistle (*Salsola kali* L.), and tumble mustard (*Sisymbrium altissimum* L.), one non-native perennial grass; crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), and two native perennial grasses; Squirreltail (*Elymus elymoides* (Raf.) Swezey) and Sandberg bluegrass (*Poa secunda* J. Presl). Crested wheatgrass was only present at the upper site.

Results

Mean monthly precipitation in 2009 was lower in every month relative to the 30-year mean except June, when precipitation was more than two-fold higher (Fig. 3) (WRCC 2011). In contrast, mean monthly precipitation in 2010 was lower than the 30-year mean for every month. Mean monthly temperatures in 2009 and 2010 were generally comparable to the 30-year means (Fig. 4) (WRCC 2011). However, temperature trends in both 2009 and 2010 were slightly below the 30-year mean until July, when they exceeded the 30-year mean.

Relationships between soil properties and downy brome abundance

Principal component axes 1 and 2 explained 31.6 and 45.8% of the total variation among sampling plots at the upper research site and 30.6 and 46.3 of the total variation at the lower research site, respectively. At the upper research site, factor loadings for downy brome and sand were similarly correlated in a positive fashion with axis 2 (Fig. 5). Alternatively, soil water content was negatively correlated with axis 2, bi-polar to downy brome cover. Soil pH, H_20 infiltration, potassium, and nitrate were also negatively correlated with axis 2, yet were generally positively correlated with axis 1, in a direction opposite to soil EC. At the lower research site, downy brome cover was negatively correlated with axis 1, while all of the other 9 variables were positively correlated this axis, most notably soil water content, nitrate, EC, potassium, and water infiltration (Fig. 5). Variation along axis 2

was primarily demonstrated by positive correlation with pH, and negative correlation with magnesium, sand, and phosphate.

Pairwise correlations corroborated with principle components/factor analyses, illustrating the negative association between downy brome abundance and both soil water content and nitrate at both research sites (Fig. 6). The negative pairwise correlations between downy brome and both EC and magnesium also agrees with how these variables were primarily bi-polar with principle components axis 1 at the lower site.

The relationship between downy brome and soil electrical conductivity was further evaluated at the lower research site (Fig. 7). The negative, logarithmic trend of downy brome cover with electrical conductivity agrees with the data presented in both the PCA as well as the pairwise correlations results. Our results identify that there may be a threshold where the electrical conductivity is too high for downy brome to reach its full potential, which is at the level of 1.2 dS m^{2-1}.

Effects of independent and combined control treatments

Downy brome cover significantly depended on the year by burn interaction at both research sites (Table 2). For the no-burn treatment, downy brome cover more than doubled between 2009 and 2010 at the upper site (Fig. 8). In contrast, downy brome cover was comparable in 2009 and 2010 within the burn treatment, and was significantly reduced by burning in 2010 at the upper site. Burning also significantly reduced downy brome cover at the lower site in 2010, but only in the herbicide

treatment (Fig. 9). Accordingly, reductions in downy brome cover between 2009 and 2010 were only significant with the combination of burning and herbicide.

The percentage of bare ground was not significantly affected by any factor at the lower site; however, the burn by year interaction was the primary factor explaining variation in bare ground at the upper site (Table 2). While bare ground decreased between 2009 and 2010 in the no-burn treatment, it more than doubled in the burn treatment, significantly increasing above the no-burn treatment in 2010 (Fig. 10). Similarly, percentage litter cover decreased between 2009 and 2010 in the no-burn treatment; however, this decrease was twice as pronounced in the burn treatment, which resulted from a significant decrease from the no-burn treatment in 2010 (Fig. 11). Percentage litter cover at the lower site similarly decreased between years with the exception of the combined treatments of burn and herbicide--the only combination to significantly reduce downy brome cover at this site (Figs. 9, 12).

Soil water content at both research sites was significantly impacted by the year by herbicide interaction (Table 2). While the largest difference in soil water was observed between 2009 and 2010, the relatively small increase with herbicide relative to the no-herbicide treatment in 2010 was also significant (Fig. 13). Soil nitrate at the upper site was dependent on interactions between year and both burning and herbicide (Table 2). Although soil nitrate at the upper site was inherently higher ($P < 0.1$) in units assigned to the no-burn relative to the burn treatment before treatments were applied in 2009, soil nitrate significantly decreased between 2009 and 2010 in the no-burn treatment where downy brome had increased during this timeframe (Figs.

8, 14). In contrast, the difference between 2009 and 2010 for soil nitrate in the burn treatment was not significant, as soil nitrate was greater in the burn relative to the non-burn treatment in 2010. Soil nitrate was also impacted by the herbicide by year interaction at both sites (Table 2). Much like the effects of burning, without herbicide to reduce downy brome abundance, soil nitrate significantly declined between 2009 and 2010, and variability between years was less pronounced or not significant (lower site) in the herbicide treatment (Fig. 15).

Influence of control treatments on resident species abundance

For the untreated control, bur buttercup cover significantly increased between 2009 and 2010 at the upper site, whereas nearly all treatments prevented this increase, with the exception of the mow and burn+mow treatment (Fig. 16). In contrast, at the lower site, bur buttercup cover was significantly greater in 2010 than 2009 only in the burn and burn+mow treatments. Russian thistle also significantly increased between 2009 and 2010 at the upper site, except for the burn, burn+herbicide and burn+herbicide+mow treatments (Fig. 17). No distinct patterns were observed for Russian thistle cover at the lower research site. Tumble mustard cover was not significantly different between 2009 and 2010 at either research site (Fig. 18); however, the burn+herbicide, herbicide+mow, and burn+herbicide+mow treatments resulted in significantly lower tumble mustard cover in 2010 than 2009.

Crested wheatgrass cover at the upper site generally increased between 2009 and 2010; however, this increase was significant only for the burn+herbicide+mow

treatment (Fig. 19). Treatment differences between years for squirreltail cover were significant only at the lower site, where all treatments that included burning had greater cover in 2009 than 2010 (Fig. 20). In contrast, Sandberg bluegrass cover increased between 2009 and 2010 at both sites only for the burn+mow treatment (Fig. 21). However, because it increased during this timeframe in the untreated control at the lower site, the responses for Sandberg bluegrass are likely spurious.

Discussion

Stable soil nutrient availability is necessary to reduce annual grasses and promote the dominance of perennial species (Huenneke et al. 1990; Harper and Belnap 2001). Consequently, restoration practices should seek to stabilize soil resource fluctuations and increase perennial plant cover (Suding et al. 2004; Sheley et al. 2010). My characterization of the relationships between downy brome abundance and soil resources, and the determination of how control treatments simultaneously impact these resources, provides a critical assessment of how contemporary annual grass management strategies impact fluctuating resource availability, which is a theoretical mechanism of annual grass dominance within plant communities (Davis et al. 2000).

Relationships between soil properties and downy brome abundance

As predicted, there was a high degree of variability within the two research sites, even though sampling plots initially appeared uniform and were located in patches dominated by exotic annual species. This heterogeneity among sampling

plots was explainable by two disparate factors: 1) the abundance of downy brome and its influence on soil resource availability and 2) how inherent differences in soil physiochemical properties influence downy brome abundance. The association of downy brome abundance and critical soil resources with the principle component axes and direct pairwise correlations between these variables clearly indicate that downy brome can greatly reduce both soil water and nitrate availability within localized patches. Others have also identified that there is a high abundance of soil nitrate in soils beneath downy brome (Norton et al. 2004; Blank 2008; Johnson et al. 2011) as well as a high nitrate uptake rate (Leonard et al. 2008) and reduced nitrate abundance throughout the growing season in downy brome invaded soils (Booth et al. 2003; Monaco et al. 2003). Consequently, downy brome is capable of creating a self serving feedback cycle with the soils it occupies by first diminishing these soil resources when they are most abundant in early spring (Leonard et al. 2008), flourishing until resources are exhausted (Ryel et al. 2010), and increasing its abundance by inputing low leaf C:N litter back into the soils that it occupies (Evans et al. 2001; Blank 2008). These results confirm that as the dominant invasive plant species, downy brome functions as an ecosystem driver, directly controlling resource availability (Evans et al. 2001; Belnap et al. 2001; Adair and Burke 2010). Plant species that germinate, or begin growth, after downy brome will thus experience unfavorable soil resource conditions for establishment and growth (Young and Evans 1972; Knapp 1992). For example, others have reported that downy brome abundance can directly interfere with the establishment of seeded revegetation species, thus

reducing their performance (Buman et al. 1988; Waldron et al. 2005). For this reason, the most drought tolerant perennial grasses generally establish better when emerging within downy brome infested areas (Asay et al. 2001).

Downy brome not only directly influences soil resources, but its abundance appears to be associated with certain soil physiochemical properties. At the upper site downy brome abundance was not limited by any inherent soil property, and can likely exist at its full biological potential in these well-drained soils (high sand content). In contrast, the negative correlation between downy brome abundance and soil EC, and the importance of soil EC and pH along the same principle components axis at the lower site, indicates that maximum downy brome abundance may be limited by certain inherent soil properties. The further examination of downy brome and electrical conductivity at the lower research site suggests that there may be a threshold where the electrical conductivity is too high for downy brome to achieve its full growth potential. The lower site is more typical of a salt desert shrub community where downy brome dominance can be confined to dense patches, under nurse plants, with the existence of distinct interspaces between these patches where soils are devoid of vegetation (Meyer et al. 2001; Jessop and Anderson 2007). Although a significant negative correlation was not observed between downy brome abundance and water infiltration, these two variables loaded in opposite directions along a principle components axis at the lower site. Infiltration rates depend on soil surface physical characteristics (e.g., surface roughness bulk density), which are generally lower in sites dominated by downy brome than sites dominated by native shrubs

(Norton et al. 2004; Boxell and Drohan 2009). Thus, soil physiochemical properties more strongly influenced downy brome abundance at the lower than the upper site.

Effects of independent and combined control treatments

Although primarily for the upper site, as predicted, control treatments to reduce downy brome, increased soil nitrate and water availability and reduced interannual variability of soil resources. The increase in soil resources was clearly associated with resource accumulation in the absence of downy brome, whose uptake of soil water and nitrate are known to be very high in early spring (D'Antonio and Vitousek 1992; Leonard et al. 2008; Ryel et al. 2010). An impressive aspect of my study was how the increase in downy brome between 2009 and 2010 in the absence of control treatments led to greater than four-fold difference between these years in soil nitrate at the upper site. In contrast, reducing downy brome abundance by nearly 40% with burning completely eliminated interannual variability for nitrate. My results agree with others who have observed drastic alterations to nutrient availability when downy brome abundance is reduced (Hull 1963; Evans and Young 1984; Blank and Young 2004; Chambers et al. 2007; Rau et al. 2007). My results also indicate that resident species were not able to entirely take advantage of the increase in resources associated with downy brome control. This suggests that resident species were not as effective at acquiring resources as downy brome; this may have occurred because overall resident species abundance was low or resident species may have been negatively impacted by control treatments. Nonetheless, the consequences of

increased resource availability are most likely positive for resident species, because resource availability increased during a critical time period when other cool season species are rapidly growing. For example, Mazzola et al. (2010) found that when downy brome propagule abundance was reduced, native species cover and density increased. Based on these results, it is plausible that if resident species propagules are abundant within a site, and they are not negatively impacted by control treatments, they could effectively take advantage of the increased resource availability. Aside from overall resource availability, it is uncertain how lower interannual variability in resources may differentially facilitate the recovery of resident species and the establishment of seeded perennial grasses. Theoretically, sites should be less invasible when resource fluctuation is minimized with the assistance control treatments (Tilman 1997; Davis et al. 2000; Chambers et al. 2007), yet overall site stability will likely require resident or seeded species to increase in abundance and provide greater control over resource dynamics at the site.

In addition to being the most effective treatment to reduce downy brome cover at the upper site, burning also strongly influenced the important soil surface characteristics of litter abundance and bare ground cover more so than herbicide application and mowing. My results for mowing conflict with others who found this method to negatively impact litter accumulation and seed input of annual grasses back into the seed bank (Wilson and Clark 2001; Seabloom et al. 2003). Negligible impacts of mowing in my study can be attributed to high precipitation and favorable growing conditions following the mowing event in the spring of 2009, and the

regrowth of downy brome. Furthermore, the inability of my herbicide application to reduce litter is a consequence of chemical treatments being incapable of *directly* influencing litter removal as burning does; rather its capacity to reduce litter is mediated *indirectly*, by how it impacts downy brome growth, seed production, and seedling emergence from seed banks. Thus, because herbicide and mowing did not effectively reduce downy brome when applied alone, and herbicide application was only important at the upper site where it reinforced the effectiveness of burning, it is not surprising that these two treatments had inconsequential influence on litter and bare ground values.

In clear contrast, lower litter and greater bare ground cover in response to fire has previously been observed in many ecosystems, including the Australian grasslands and the grasslands and shrublands of the western US (Ford and Johnson 2006; Jessop and Anderson 2007; Prober et al. 2008). It has also been observed that burning directly influences the abundance of downy brome and initiates changes in plant species composition by altering the seedbed conditions for germination of resident species. Species like downy brome with affinity to germinate in high litter cover will be most impacted by burning (Piemeisel 1951; Evans and Young 1984). A weakened stand of downy brome and the creation of bare ground via burning may also assist with altering species composition by creating a suitable seedbed for revegetation (Call and Roundy 1991; DiTomaso et al. 2006), reducing inevitable downy brome competition with revegetation species (Melgoza et al. 1990), and increasing soil contact with herbicides that are most effective when applied to bare

soils (Monaco et al. 2005; Kyser et al. 2007). Consequently, burning, whether alone or in combination with other treatments, appears to be the best option for reducing downy brome abundance, modifying soil surface characteristics, and species composition at these salt desert shrubland sites.

Influence of control treatments on resident species abundance

Direct discussion of how downy brome control treatments impacted resident species is not possible for a couple of reasons. Firstly, individual resident species typically made up less than 2% of the plant community and they did not greatly increase when downy brome was reduced in any of the treatments. Secondly, similar to litter and bare ground cover, resident species did not consistently respond to treatments at the upper and lower sites. Consequently, I only can address the manner in which independent treatments influenced the interannual abundance of Russian thistle at the upper site, and bottlebrush squirreltail at the lower site relative to the control with confidence.

Litter removal and a high proportion of bare ground are known to create ideal conditions for Russian thistle (Young and Evans 1972; Khan et al. 2002). The manner in which Russian thistle responded at the upper site must be qualified by the fact that background litter cover (within the no-burn treatment), was significantly higher in 2009 than 2010. Thus, it makes sense that Russian thistle cover significantly increased during this timeframe within the control and many treatments, even though these treatments did not directly reduce litter cover. Burning should have amplified

this response by its clear removal of litter, but instead, when applied alone and in combination with herbicide and mowing, it generally dampened the background increase in Russian thistle, most likely by consuming seeds on the soil surface as well as seeds that had not fallen from late-maturing plants. As a typical warm-season and tumbleweed species, seeds remain on plants until they are primarily dispersed in late fall when the aboveground portion is broken and travels with the wind (Allen and Knight 1984; Stallings et al. 1995). Thus, if fires occur before dispersal of seeds, it can directly impact successional trajectories of a site by reducing opportunities for Russian thistle to reestablish on bare soil, and by consuming litter accumulation that typically has been shown to assist downy brome establishment and replacement of Russian thistle in the years following disturbance (Piemeisel 1951; Evans and Young 1970; Young and Evans 1973).

The manner in which bottlebrush squirreltail increased in treatment combinations that included burning illustrates that effective downy brome control in areas with some residual native vegetation can have important consequences for site resiliency, as has been shown for medusahead infestations (Davies *in press*). By fostering the productivity of this bunchgrass species, it may gain ground previously occupied by downy brome, and while becoming more abundant, it may impede future invasion. When abundant, cool season bunchgrasses can resist invasion (Davies et al. 2010; McGlone et al. 2011) because they utilize resources at similar times and offer competition to invasive plant species (James 2008; Leonard et al. 2008; Leffler et al. *in press*). In addition, when burning occurs late in the season as it did in my plots, fire

poses only a minor disturbance to bottlebrush squirreltail (Wright 1971; Young and Miller 1985), yet clearly impacted downy brome abundance. Finally, others have observed bottlebrush squirreltail colonizing and replacing downy (Hironaka and Tisdale 1963; Hironaka and Sindelar 1973), which may be associated with its rapid growth rate and performance as a seedling or competitive ability in larger, mature plants (Young and Mangold 2008; Leger 2008; Parsons et al. *in press*). In addition, the increase in soil nitrate where downy brome was controlled may also have facilitated the growth of bottlebrush squirreltail as has been suggested by McGlone et al. (2011). In sum, bottlebrush squirretail responded favorably to burning, which emphasizes its growing importance as a revegetation species in fire-prone, or disturbed areas (Simmons and Rickard 2002). However, given the low cover of bottlebrush squirreltail as well as all of the perennial grasses at my research sites, revegetation to artificially increase the abundance of this important functional group appears to be necessary to prevent invasive annual species from regaining site dominance in the future (Monaco et al. 2005; D'Antonio et al. 2009; Morris et al. 2009).

Implications

Managing downy brome-invaded shrublands is extremely challenging, however as the relationships between downy brome and the soil it occupies are further studied and the correct tools are implored for downy brome management, outcomes may be improved (Sheley et al. 2010). The results of this study showcase the importance of

the relationships between downy brome and soil nutrients on invaded salt desert shrublands and demonstrate that downy brome strongly influences water and nitrate availability. In addition, burning and herbicide application both effectively reduced resource fluctuation and increased the availability of soil water and nitrate as has been observed in other regions (Chambers et al. 2007; Adair et al. 2008), yet burning was by far the most overall effective treatment to reduce downy brome abundance, interannual fluctuation, and prepare the soil surface for seeding desirable species. My results imply that the only real strategy to avoid reinvasion and maintain site stability by reducing resource fluctuation is to establish perennial species. Resident species at my sites, and most likely others dominated by downy brome within the Great Basin are incapable of entirely filling the void when downy brome is controlled. Thus, the "window of opportunity" created by weakening downy brome and stabilizing resource availability must coincide with successful establishment of perennial species, that over time can gain dominance and begin to control plant-soil dynamics.

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Table 1. Results of ANOVA for cover (downy brome, bare ground, and litter) and three soil measures at two research sites. Significant effects are indicated with bolded *P-values* (*P* = 0.1); non-significant effects = *NS*.

Model Effect	*df*	Downy brome	Bare ground	Litter	Soil H_20	Soil pH	Nitrate
Upper Site							
Burn	2	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Herbicide	2	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Mowing	4	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Herb	2	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Mow	4	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Herb*Mow	4	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Herb*Mow	4	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Year	8	**0.0257**	*NS*	**<.0001**	**<.0001**	**0.0030**	**0.0011**
Burn*Year	8	**0.0124**	**0.0005**	**0.0113**	*NS*	*NS*	**0.0064**
Herbicide*Year	8	*NS*	*NS*	*NS*	**0.0105**	*NS*	**0.0073**
Mowing*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Herb*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Mow*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Mow*Herb*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Herb*Mow*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Lower Site							
Burn	2	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Herbicide	2	*NS*	*NS*	*NS*	*NS*	*NS*	**0.0687**
Mowing	4	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Herb	2	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Mow	4	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Herb*Mow	4	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Herb*Mow	4	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Year	8	**0.0029**	*NS*	**0.0010**	**<.0001**	**<.0001**	*NS*
Burn*Year	8	**0.0250**	*NS*	*NS*	*NS*	*NS*	*NS*
Herbicide*Year	8	**0.0797**	*NS*	*NS*	**0.0131**	*NS*	**0.0650**
Mowing*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Herb*Year	8	**0.0293**	*NS*	**0.0858**	*NS*	*NS*	*NS*
Burn*Mow*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Mow*Herb*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Burn*Herb*Mow*Year	8	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*

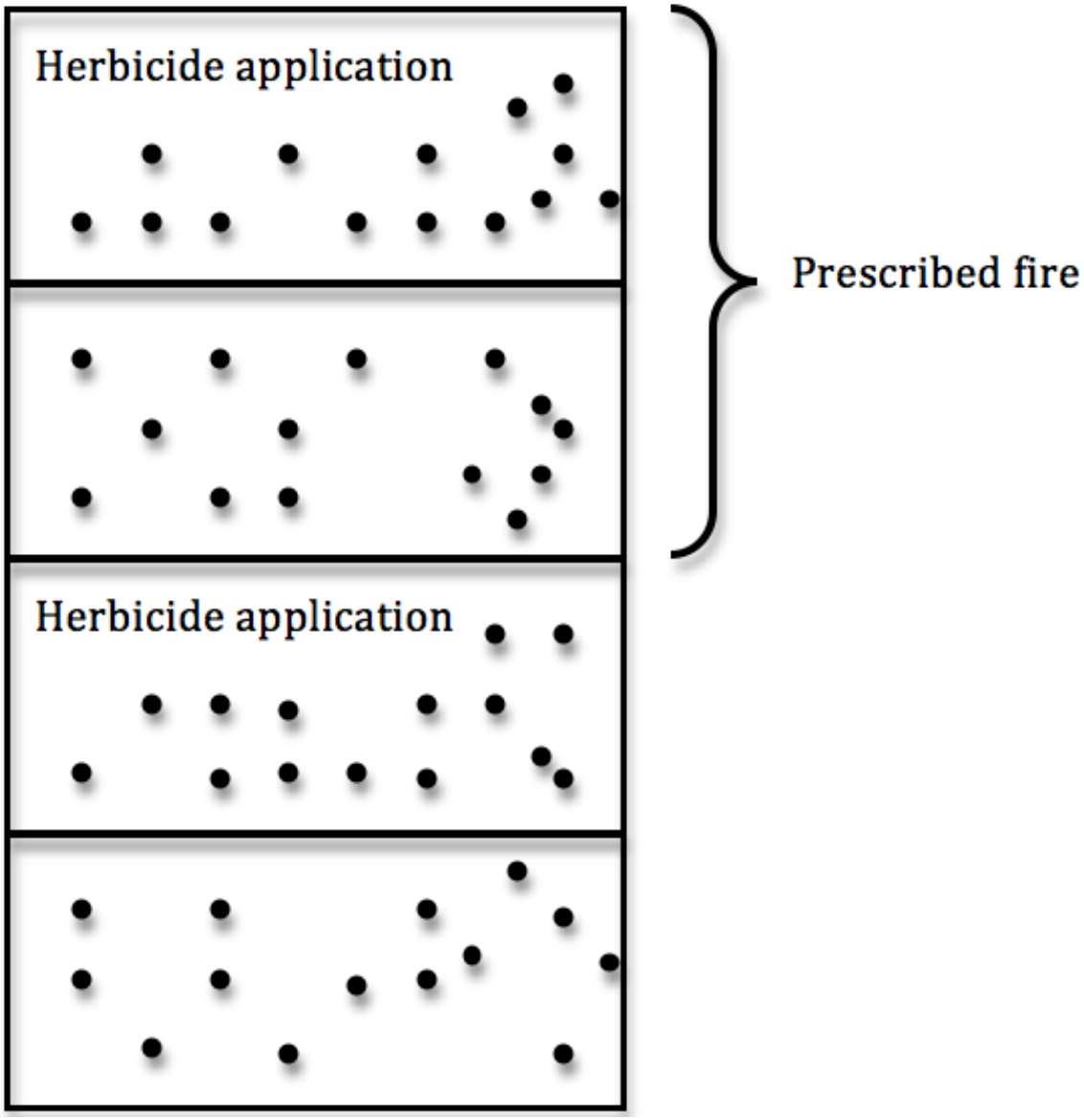

Figure 2. Diagram of split-plot design used to apply prescribed fire and herbicide to land units. Each unit contained 14 sampling plots, 7 of which were randomly assigned to a mowing treatment.

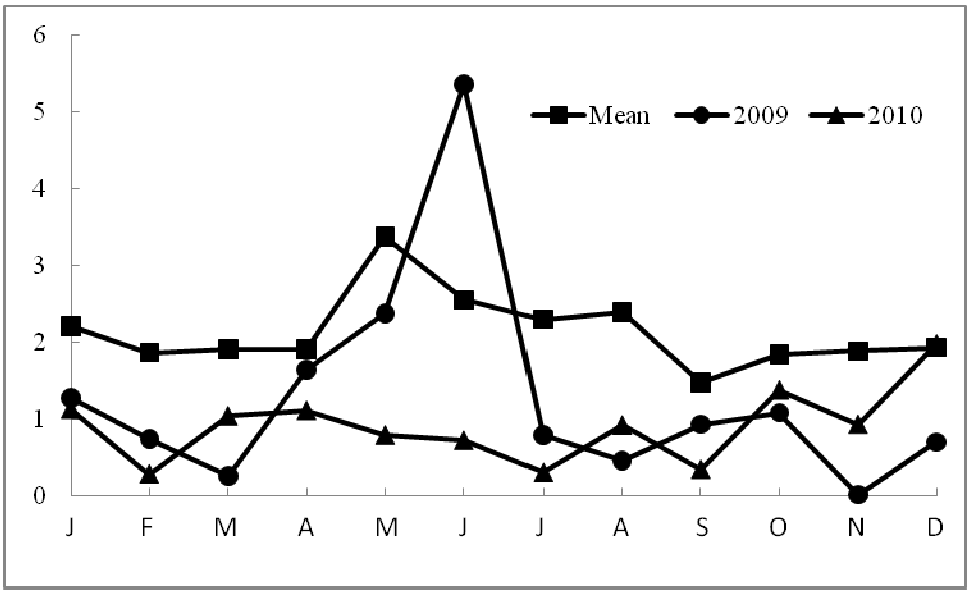

Figure 3. Mean monthly precipitation for Park Valley, Utah in 2009 and 2010. The long-term mean represents the 30-year mean (WRCC 2011).

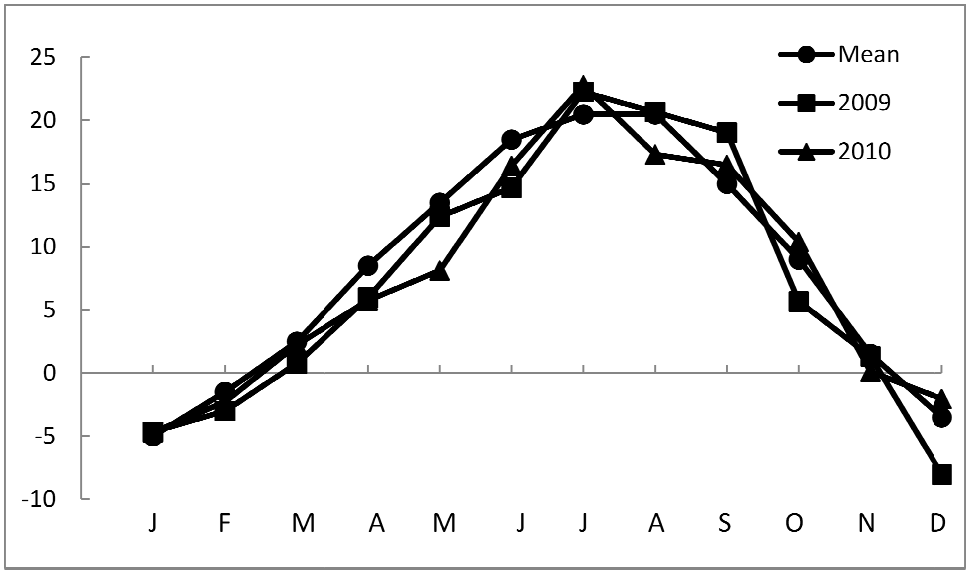

Figure 4. Mean monthly air temperature for Park Valley, Utah in 2009 and 2010. Long-term monthly means represents the 30-year mean (WRCC 2011).

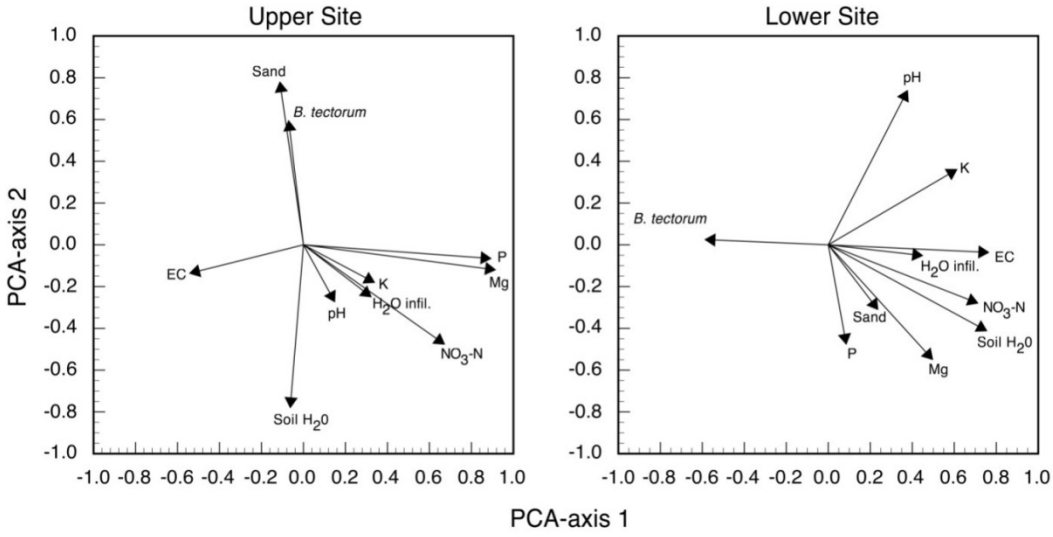

Figure 5. Correlation between factor loadings (downy brome cover [*B. tectorum*] and the nine soil variables) for two research sites in Park Valley, Utah. Analyses were performed with principle components analysis (PCA) and common factor analysis.

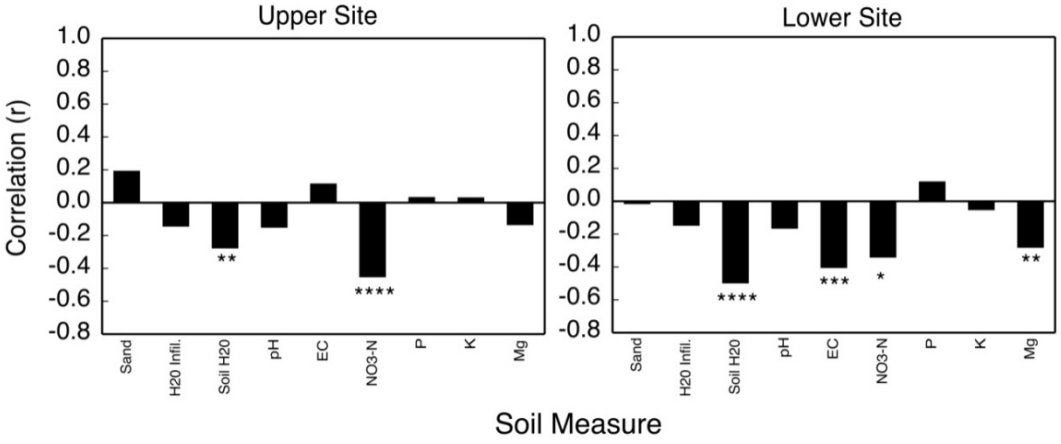

Figure 6. Pairwise correlations between downy brome cover and nine soil variables at two research sites in Park Valley, Utah. *P-values* are inicated as *< 0.05, **< 0.01, ***< 0.001, and ****< 0.0001.

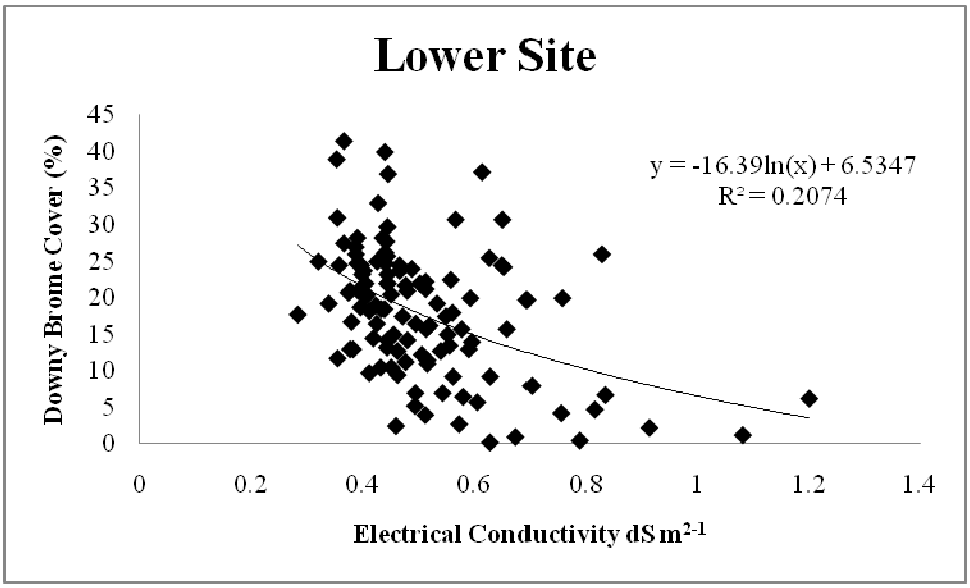

Figure 7: Relationship between downy brome cover and electrical conductivity at the lower research site.

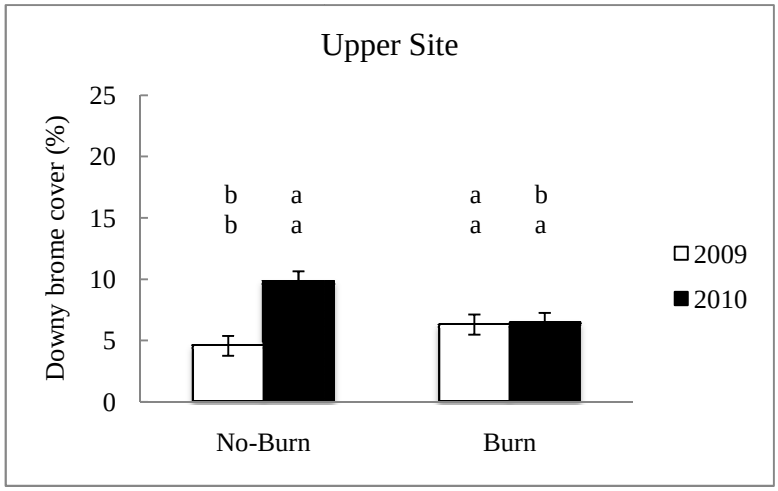

Figure 8. Mean (n = 2 ± 1 *SE*) percentage downy brome cover at the upper research site. Upper letters indicate difference between treatments within a year; lower letters indicate difference between years within a treatment ($P < 0.1$).

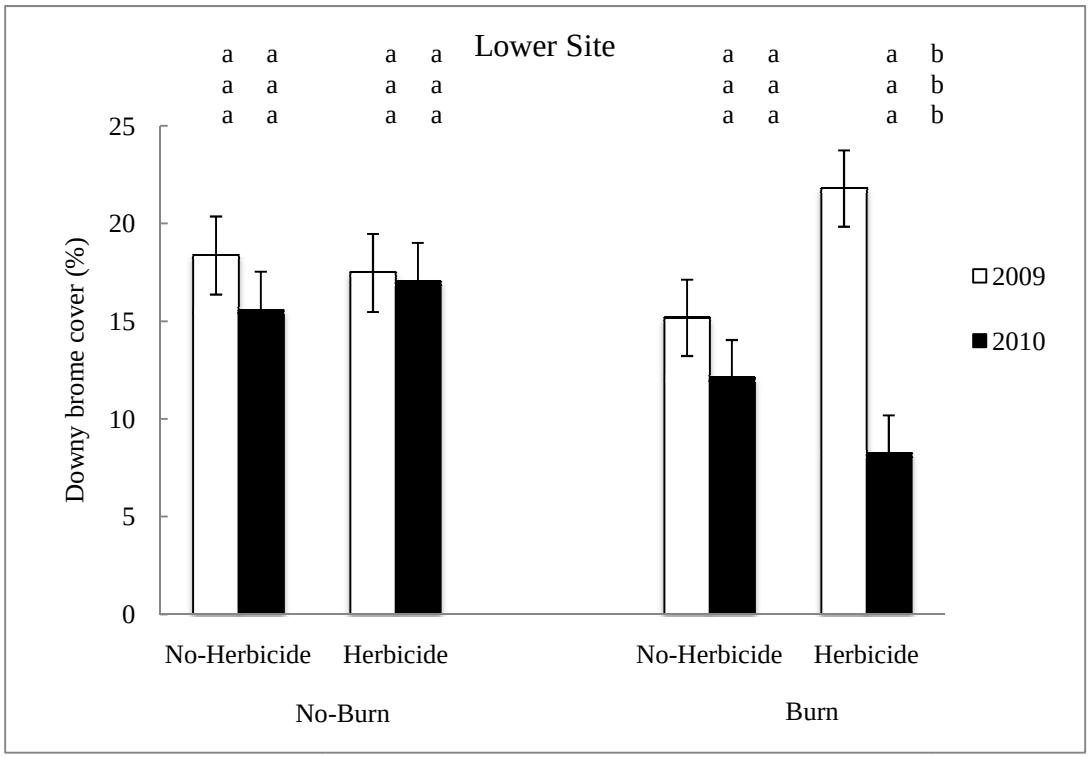

Figure 9. Mean (n = 2 ± 1 *SE*) percentage downy brome cover at the lower research site. Upper letters indicate difference between burn treatments within a year and herbicide treatment; middle letters indicate difference between herbicide treatments within a year and burn treatment; lower letters indicate difference between years within a burn and herbicide treatment ($P < 0.1$).

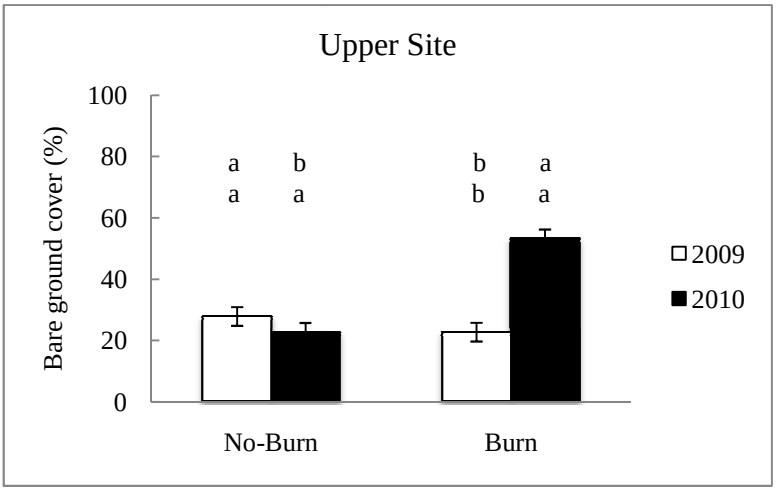

Figure 10. Mean (n = 2 ± 1 *SE*) percentage bare ground cover at the upper research site. Upper letters indicate difference between treatments within a year; lower letters indicate difference between years within a treatment ($P < 0.1$).

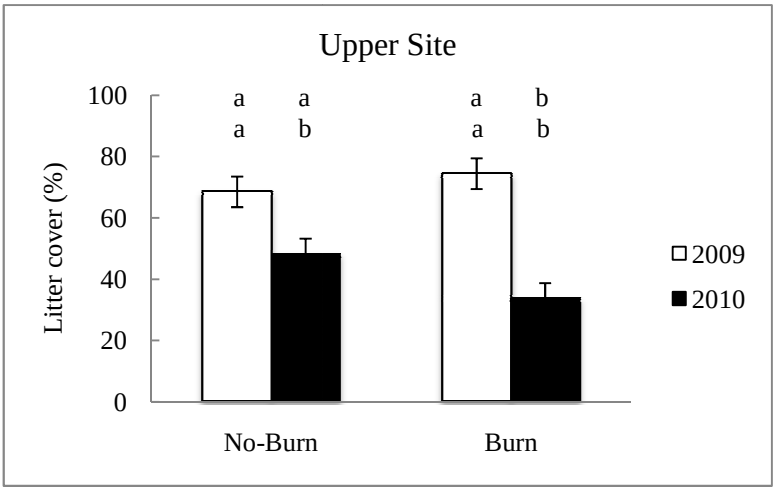

Figure 11. Mean (n = 2 ± 1 *SE*) percentage litter cover at the upper research site. Upper letters indicate difference between treatments within a year; lower letters indicate difference between years within a treatment ($P < 0.1$).

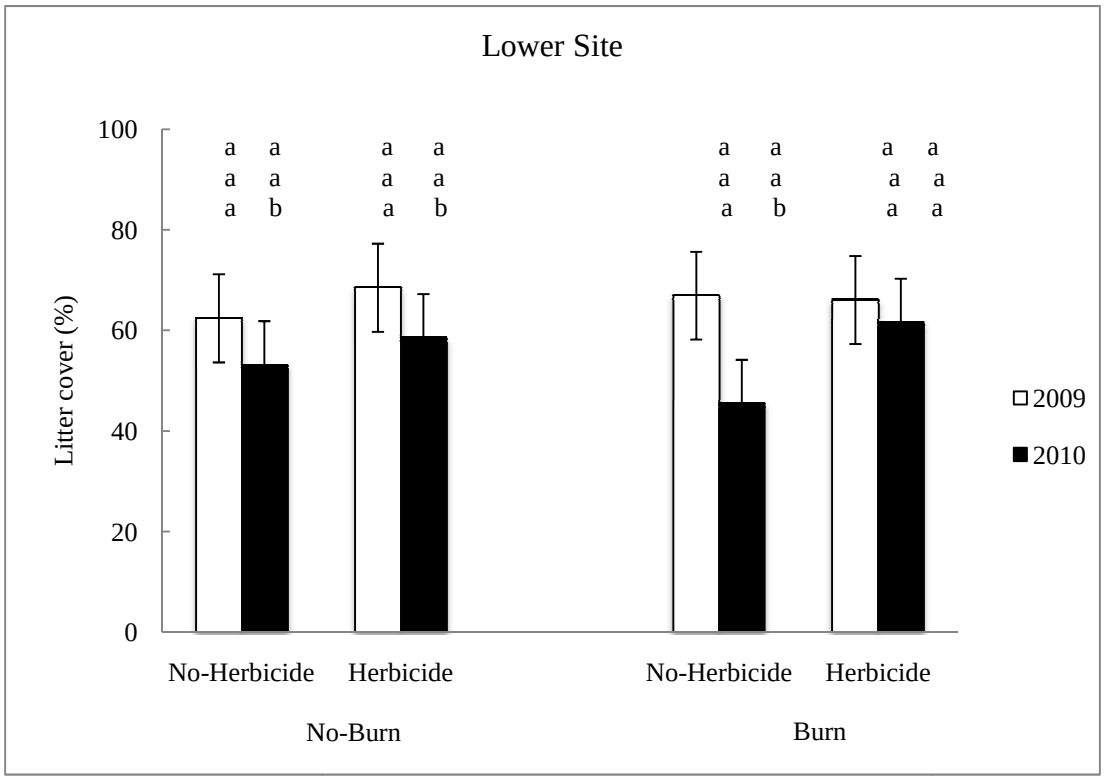

Figure 12. Mean (n = 2 ± 1 *SE*) percentage litter cover at the lower research site. Upper letters indicate difference between burn treatments within a year and herbicide treatment; middle letters indicate difference between herbicide treatments within a year and burn treatment; lower letters indicate difference between years within a burn and herbicide treatment ($P < 0.1$).

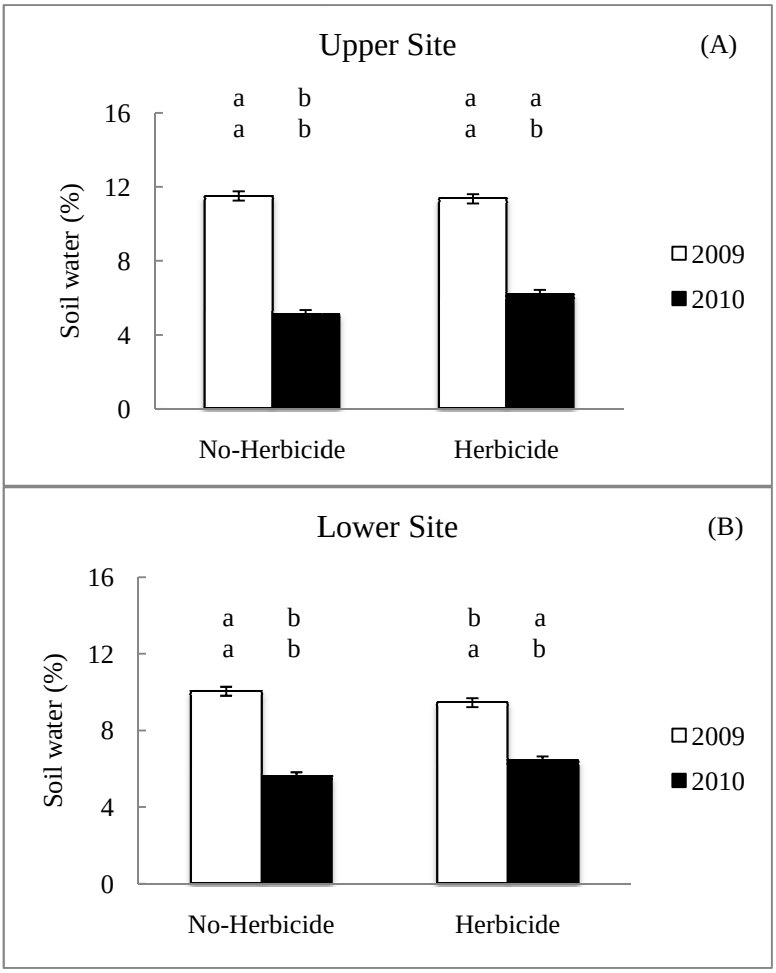

Figure 13. Mean (n = 2 ± 1 *SE*) percentage soil water at two research sites. Upper letters indicate difference between treatments within a year; lower letters indicate difference between years within a treatment ($P < 0.1$).

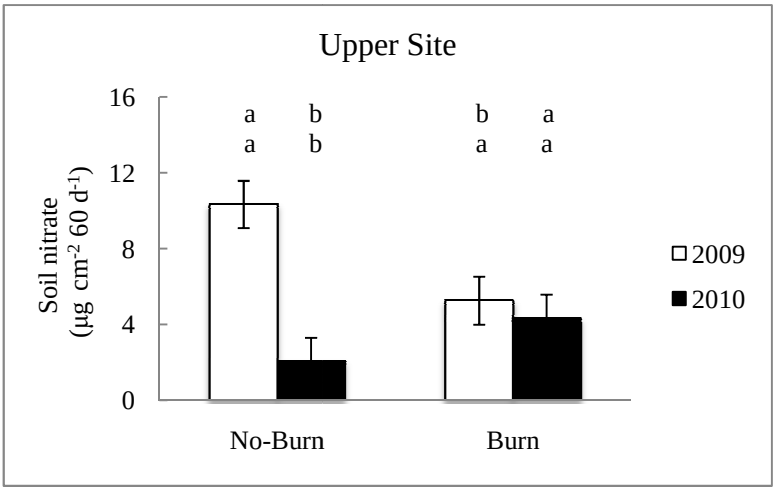

Figure 14. Mean (n = 2 ± 1 *SE*) 60-d soil nitrate accumulation at the upper research site. Upper letters indicate difference between treatments within a year; lower letters indicate difference between years within a treatment ($P < 0.1$).

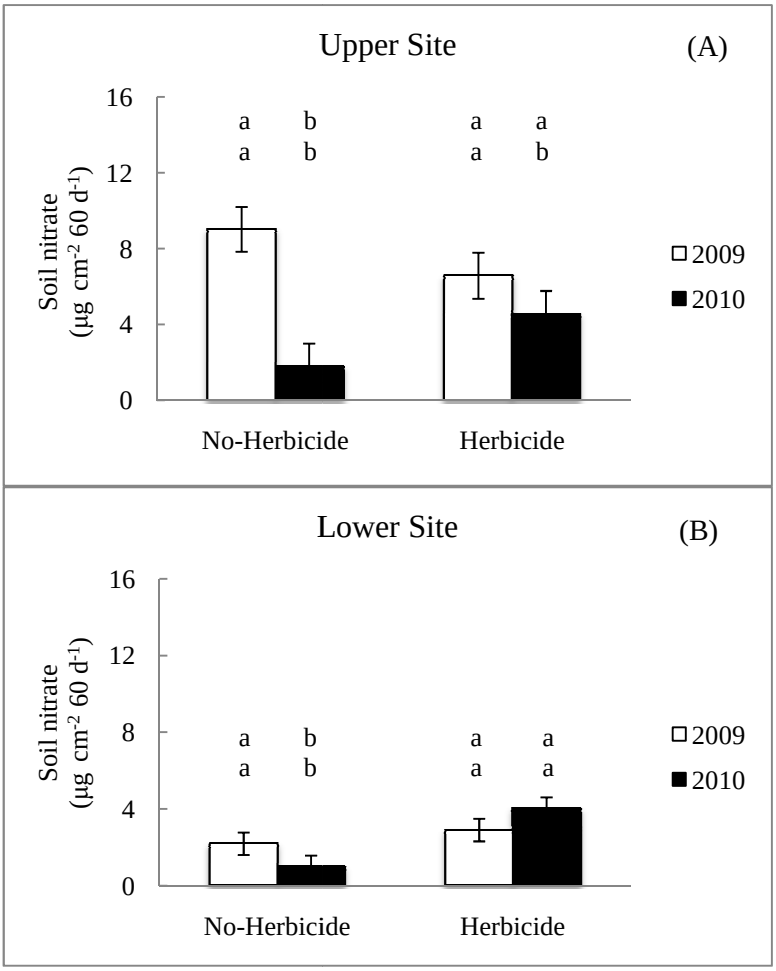

Figure 15. Mean (n = 2 ± 1 *SE*) 60-d soil nitrate accumulation at the two research sites. Upper letters indicate difference between treatments within a year; lower letters indicate difference between years within a treatment ($P < 0.1$).

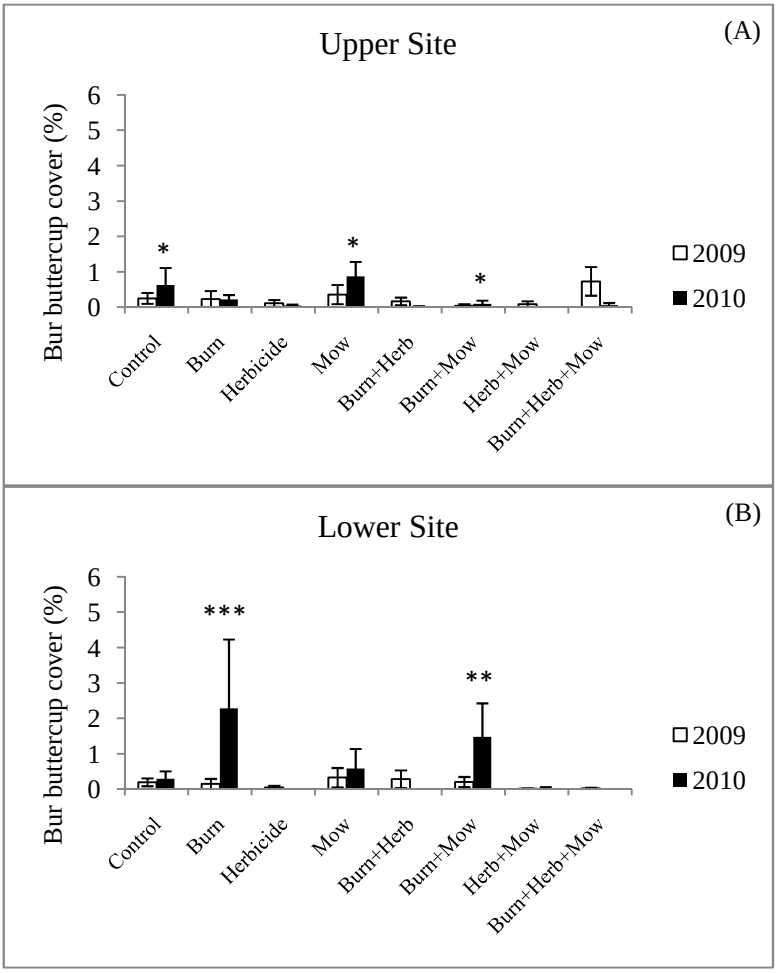

Figure 16. Mean (n = 14 ± 1 *SE*) percentage bur buttercup cover in consecutive years at two research sites. Asterisks indicate significant Wilcoxon sign rank tests (df = 13) comparing 2009 and 2010 (*< 0.1, **< 0.05, and ***< 0.01).

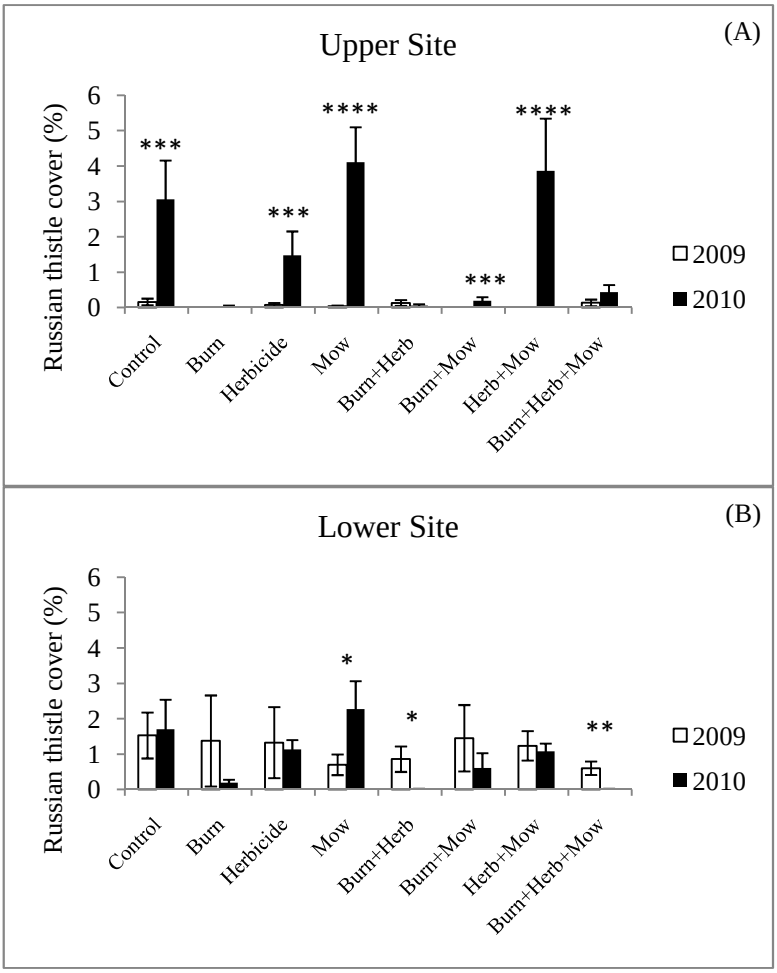

Figure 17. Mean (n = 14 ± 1 *SE*) percentage Russian thistle cover in consecutive years at two research sites. Asterisks indicate significant Wilcoxon sign rank tests (df = 13) comparing 2009 and 2010 (*< 0.1, **< 0.05, ***< 0.01, and ****< 0.001).

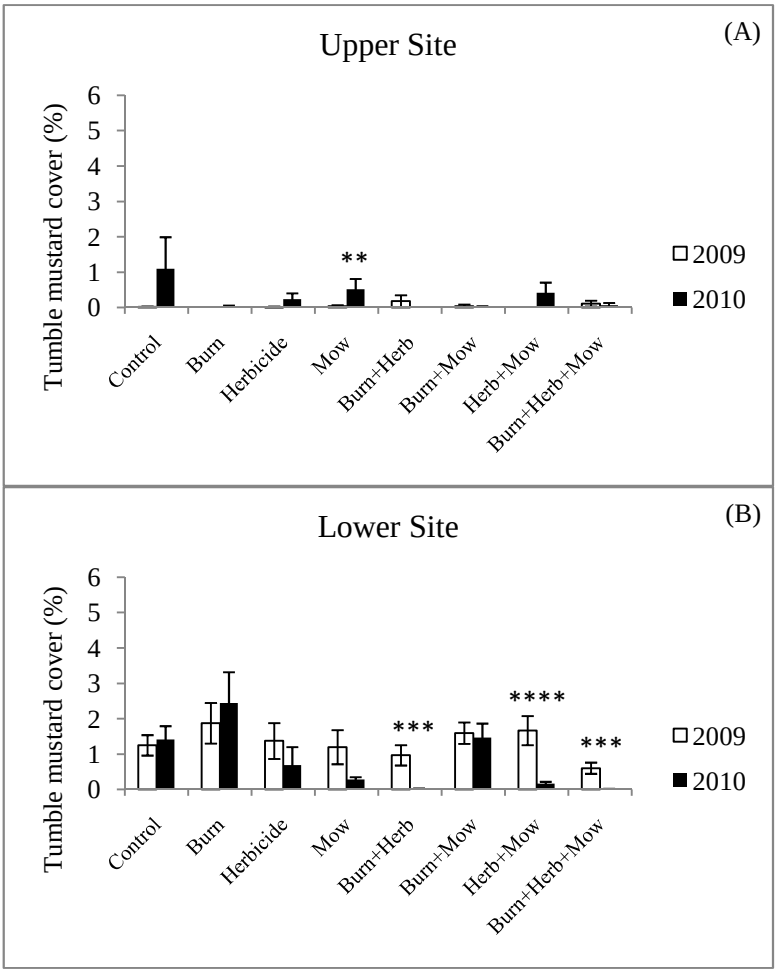

Figure 18. Mean (n = 14 ± 1 *SE*) percentage tumble mustard cover in consecutive years at two research sites. Asterisks indicate significant Wilcoxon sign rank tests (df = 13) comparing 2009 and 2010 (*< 0.1, **< 0.05, ***< 0.01, and ****< 0.001).

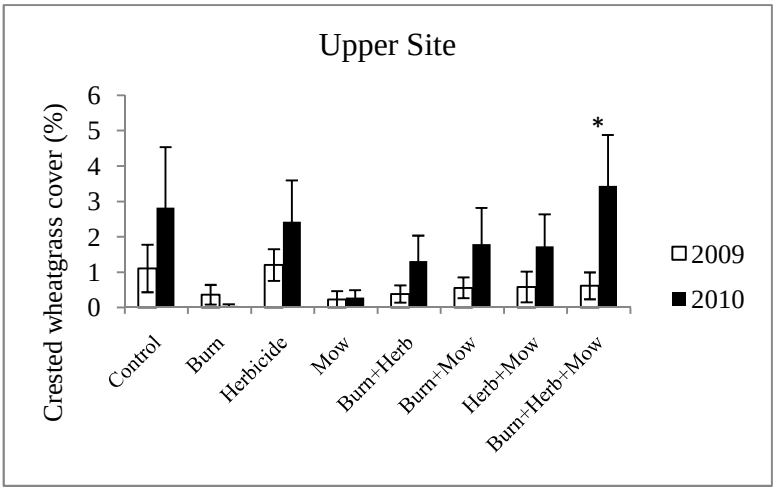

Figure 19. Mean (n = 14 ± 1 *SE*) percentage crested wheatgrass cover in consecutive years at two research sites. Asterisks indicate significant Wilcoxon sign rank tests (df = 13) comparing 2009 and 2010 (*< 0.1, **< 0.05, ***< 0.01, and ****< 0.001).

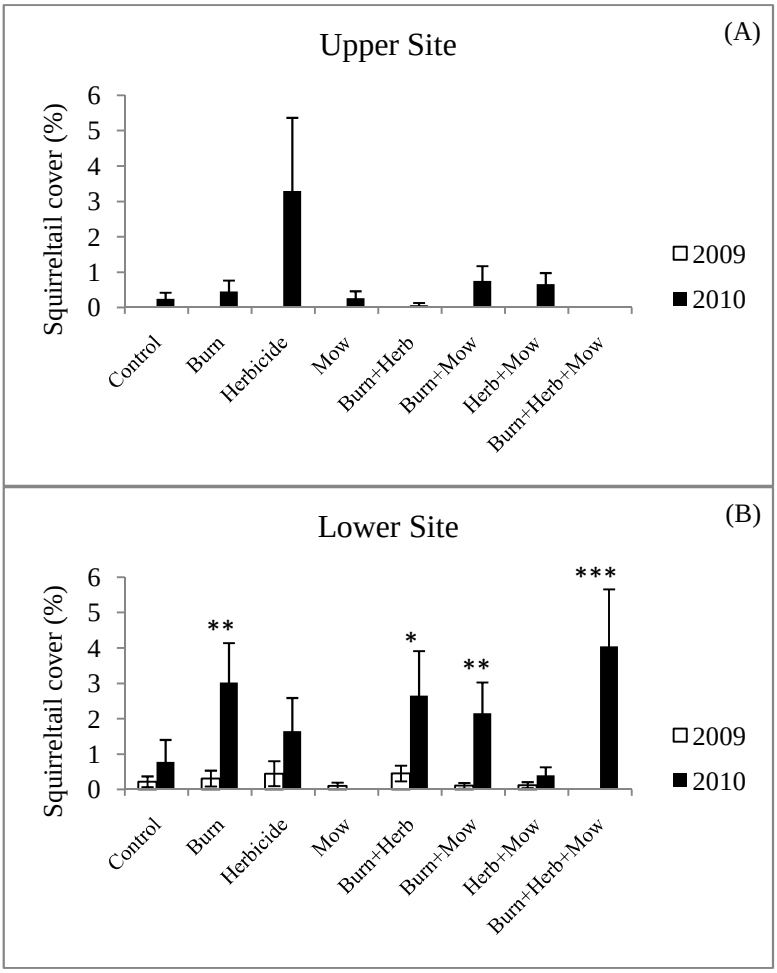

Figure 20. Mean (n = 14 ± 1 *SE*) percentage squirreltail cover in consecutive years at two research sites. Asterisks indicate significant Wilcoxon sign rank tests (df = 13) comparing 2009 and 2010 (*< 0.1, **< 0.05, ***< 0.01, and ****< 0.001).

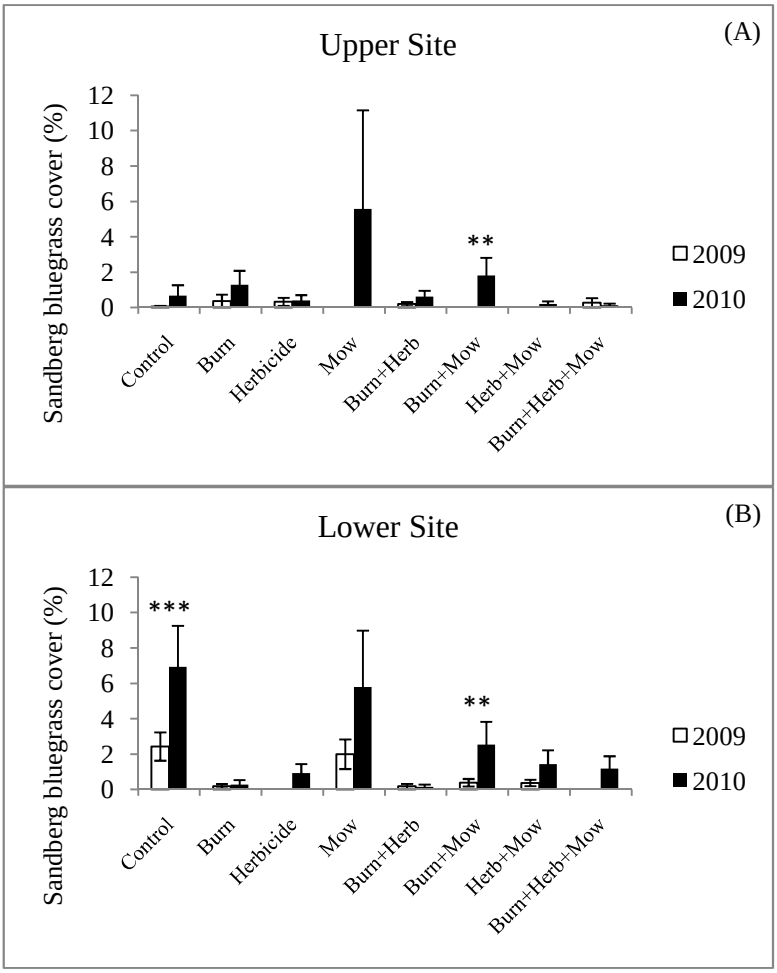

Figure 21. Mean (n = 14 ± 1 *SE*) percentage Sandberg's bluegrass cover in consecutive years at two research sites. Asterisks indicate significant Wilcoxon sign rank tests (df = 13) comparing 2009 and 2010 (*< 0.1, **< 0.05, ***< 0.01, and ****< 0.001).

CHAPTER 3

COMPARISON OF HERBICIDES FOR REDUCING ANNUAL GRASS EMERGENCE IN TWO GREAT BASIN SOILS

Abstract

Reducing seed germination and seedling emergence of downy brome (*Bromus tectorum* L.) improves the success of revegetating degraded shrubland ecosystems. While pre-emergence herbicides can potentially reduce these two processes, their impact on germination and emergence of downy brome and revegetation species in semi-arid ecosystems is poorly understood, and has not been comprehensively studied in soils with potentially contrasting herbicide bioavailability, i.e., residual plant activity. We designed a greenhouse experiment to evaluate the effects two pre-emergence acetolactate synthase (ALS)-inhibiting herbicides (rimsulfuron and imazapic) on germination and emergence of downy brome and two revegetation grass species (crested wheatgrass [*Agropyron cristatum* {L.} Gaertn.] and bottlebrush squirreltail [*Elymus elymoides* {Raf.} Swezey)]), which were grown in representative soils from salt desert and sagebrush shrublands. Pre-emergence herbicides significantly ($P < 0.05$) reduced seedling emergence and biomass production of downy brome and crested wheatgrass, and increased mortality more so in sagebrush compared to salt desert soil, suggesting that these common Great Basin soils fundamentally differ in herbicide bioavailability. Also, germination and emergence of the two highly responsive species (crested wheatgrass and downy brome) were clearly more impacted by rimsulfuron than imazapic. We discuss these results in

terms of how the specific soil physiochemical properties influence herbicide adsorption and leaching. Our results shed new light on the relative performance of these two promising herbicides and the importance of considering soil properties when applying pre-emergence herbicides to reduce germination and emergence of invasive annual grasses and create suitable seedbed conditions for revegetation.

Introduction

Invasive annual grasses have the potential to seriously impact ecosystem processes in semi-arid regions, resulting in altered structure and function that favor their continued dominance (Ehrenfeld et al. 2005). Moreover, the long-term effects of annual grass invasion are predicted to increase with time since invasion, depending on their functional distinctiveness and abundance within the ecosystem (Strayer et al. 2006). Incidentally, both functional distinctiveness and abundance of invasive grasses increase as perennial plant functional types decline with frequent wildfires fueled by high annual grass productivity (D'Antonio and Vitousek 1992; Brooks et al. 2004). Annual grass abundance is not only reinforced by altered ecosystem structure, function, and disturbance regimes, but also by a suite of dispersal and reproductive traits that perpetuate their persistence (Sakai et al. 2001; Funk et al. 2008; Moles et al. 2008). Identifying methodologies to target these traits, and their influence on key ecosystem processes, may present an ecologically-based approach to reduce the abundance of invasive annual grasses and improve revegetation success (Sheley et al. 2010).

Annual grasses persist within disturbed ecosystems by exhibiting numerous plant traits that are functionally distinct from resident native species. First, compared to perennial species, they have a shorter life span and earlier emergence, which enhance growth potential, competitive dominance, and seed production (Sutherland 2004; Verdu and Traveset 2005). Second, higher growth rate and earlier maturity enable them to more favorably respond to anthropogenic disturbance than perennial species (Corbin and D'Antonio 2004; HilleRisLambers et al. 2010), and rapidly exploit soil resources when they are most available (Garnier 1992; Seabloom et al. 2003; James et al. 2009). Combined, these traits provide mechanisms for annual plants to create three restoration obstacles: 1) persistent seed banks (Marañón 1998; Facelli et al. 2005), 2) continued dominance of annual species during community assembly (Grman and Suding 2009; James et al. *in press*), and 3) an intensely competitive environment for both resident and artificially-seeded species during revegetation (Eliason and Allen 1997; Hamilton et al. 1999; Humphrey and Schupp 2001, 2004). Addressing these obstacles by "minimizing deposits and maximizing withdrawal" from seed banks is thus a necessary precursor to reduce interference on seeded species during revegetation (Forcella et al. 1993; Eiswerth et al. 2009; Menalled and Schonbeck 2011).

Numerous measures can be used during the life cycle of annual grasses to reduce seed banks. These include early-spring targeted grazing to reduce productivity and seed production (Harmoney 2007), summer prescribed burns to consume abundant litter and seeds in leaf litter (Diamond et al. 2009; Pyke et al. 2010), and pre-emergence application of pathogens and herbicides to kill seeds and emerging

plants (DiTomaso et al. 2010; Meyer et al. 2010). Herbicides can be particularly important because if viable seeds survive to germinate and emerge, annual grasses can quickly regain dominance and directly interfere with revegetation efforts (Evans et al. 1969; Morris et al. 2009; Davies 2010).

Because pre-emergence herbicides are designed to be bioavailable within soils, many interactive factors influence their capacity to reduce germination and emergence of annual grasses. For example, soil bioavailability of acetolactate synthase (ALS)-inhibiting herbicides (e.g., sulfonylureas and imidazolinones) is strongly influenced by their organic/molecular structure and adsorption/desorption to minerals and organic matter, degradation by soil microorganisms, chemical hydrolysis, and dissipation and/or leaching from soil (Goetz et al. 1990; Loux and Reese 1993; Schneiders et al. 1993; Vicari et al. 1996; Dinelli et al. 1997). The complexity of soil bioavailability is further compounded when considering differential herbicide injury to target weeds and non-target revegetation species (Obrigawitch et al. 1998; Hollaway et al. 2006). Consequently, indentifying the underlying plant traits responsible for pre-emergence herbicide injury and clarifying how differences in soil physiochemical properties influence seed germination and emergence of invasive annual grasses will improve weed control and prevent unnecessary injury to revegetation species. Unfortunately, these processes have not been studied extensively for semi-arid rangeland ecosystems, where pre-emergence herbicide use is currently a major component of integrated weed management and revegetation on lands impacted by invasive annual grasses (Monson 2004; DiTomaso et al. 2010).

Salt desert and sagebrush shrublands of the Great Basin (western United States) are currently suffering from the impacts of annual grasses and the possibility of future expansion within the region (West 1988; Young and Longland 1996; Young and Allen 1997; Bradley 2010). In particular, dominance of the invasive annual grass downy brome (*Bromus tectorum* L.) has increased fire frequency and the widespread loss of native species (D'Antonio and Vitousek 1992; Brooks et al. 2004). Efforts to reduce downy brome dominance with integrated management prior to revegetation has had poor success across these shrublands (Robocker et al. 1976; Eiswerth et al. 2009), which differ in many characteristics including elevation, precipitation, topography, vegetation, soils, and disturbance history (West 1983a, 1983b, 1988; Knapp 1996). Thus, greater understanding of how downy brome and revegetation species respond to pre-emergence herbicide applications in contrasting Great Basin soils may improve the integrated management of invasive annual grasses in this critical region.

We designed a greenhouse experiment to evaluate the effects of two pre-emergence ALS-herbicides on germination and emergence of downy brome and two-revegetation grass species grown in representative soils from salt desert and sagebrush shrublands that potentially vary widely in herbicide soil bioavailability. Because sagebrush soils typically have higher soil organic matter, lower soil pH, and higher clay content and cation exchange capacity, we hypothesized that seed germination, seedling emergence, and seedling mortality of downy brome and perennial revegetation grasses would be reduced more by pre-emergence herbicides in sagebrush than salt desert soils. In addition, we anticipated that a detailed analysis

of germination and emergence would provide new insights into how application of pre-emergence herbicides to these soils influences downy brome injury and the performance of desirable perennial grasses. Clarifying these currently unknown factors may lead to improved herbicide applications and revegetation success for downy brome-dominated shrublands and other regions experiencing similar annual grass invasions.

Materials and Methods

Soils for a greenhouse study were obtained in May 2010 from two downy brome-dominated ecological sites in western Box Elder County, UT, near the town of Park Valley. These two semidesert ecological sites are broadly distributed in Major Land Resource Area 28A (Great Salt Lake Area) and throughout the Great Basin. Climate of this region is characterized by cold snowy winters and hot dry summers with most of the precipitation occurring through snow and spring rains ranging from 200 to 300 mm per year. Mean annual air temperature is 10°C. Parent material is derived from alluvium, originating from the canyons of the Raft River Mountains to the north.

The first ecological site is classified as semidesert alkali loam (Black greasewood [*Sarcobatus vermiculatus* {Hook} Torr.]) (lat 41°45' 25.64"N, long 113°16' 6.46"W). Soils are in the Kunzler series; classified as coarse-loamy mixed, superactive, mesic, durinodic Xeric Haplocalcids, and occur on over 100 000 ha in the Great Basin (CEI 2011). This site occurred at 1545 m elevation, on 2% slope, and a south aspect. Vegetation of this salt desert ecosystem is typically dominated by the

shrubs black greasewood, Wyoming big sagebrush (*Artemisia tridentata ssp. Wyomingensis* [Beetle & Young] S.L. Welsh), and rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird *ssp. consimilis* [Greene] G.L. Nesom & Baird). The herbaceous understory is composed of Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth) and bottlebrush squirreltail (West 1983a, 1983b). The second ecological site is classified as semidesert gravelly loam (Wyoming big sagebrush) (lat 41°49' 26.21"N, long 113°17' 25.21"W). Soils are in the Kapod and Donnardo series; classified as loamy-skeletal, mixed, superactive, mesic Calcic Argixerolls and loamy-skeletal, mixed, superactive, mesic Typic Argixerolls, which occur on over 40 000 ha in the Great Basin (CEI 2011). This site occurred at 1680 m elevation, on 3% slope, and a south aspect. Wyoming big sagebrush and other native herbaceous grasses like bluebunch wheatgrass (*Pseudoregneria spicata* [Pursh] A Löve) and bottlebrush squirreltail typically dominate this sagebrush ecosystem. At both sites, soils were excavated from to a 15 cm depth from a 2-m^2 area, sifted through a 1.25-cm^2 sieve in the field to remove debris and rocks, and thoroughly mixed.

Experimental design

In the laboratory, fifteen 2-kg soil subsamples from each ecological site were air-dried at 25˚C for 14 d, passed through a 2-mm sieve to further remove debris and gravel, and hand ground with a mortar and pestle. Soil texture was determined using the hydrometer method to quantify percentage sand, silt, and clay (Gee and Bauder 1986). Samples (40 g) were mixed with a 100-mL sodium hexametaphosphate-water solution and 250 mL of deionized water and shaken at 150 rpm for 1 h, placed into a

1-L cylinder, and filled with deionized water. A custom plunger was used to mix the slurry before measuring its temperature and density (g L^{-1}) with a Bouyoucos hydrometer (14-331-5C, Thermo Scientific, Beverly, MA) after 30 s and 1440 min. These two variables were used to determine percent sand, silt, and clay content. Soil pH was measured by mixing 15 g of soil with 30 mL of deionized water, shaking at 100 rpm for 30 min, then measuring the slurry with a pH meter (Orion 3 star bench-top pH meter, Thermo Scientific, Beverly, MA) (Thomas 1996). Total N and C were determined on 0.1 g of soil combusted with a LECO CHN 2000 Autoanalyzer (Leco Corp., St. Joseph, MI) (Wolf 1994). Electrical conductivity was determined on 50 g of soil mixed with 50 mL of deionized water, shaken at 200 rpm for 2 hrs, and filtered through a filter paper (Grade 4, Whatman International Ltd., Maidstone, England) using a vacuum system. Electrical conductivity was measured on the filtered solution with an ionic probe (Orion 3 star bench-top conductivity meter, Thermo Scientific, Beverly, MA) (Rhodes 1996). Cation exchange capacity (CEC) and organic matter content (OM) were analyzed by the Utah State University Analytical Laboratory using the $NaOAc/NH_4OAc$ replacement method for CEC, and the loss on ignition/ash method for OM (n = 5).

Soil from each ecological site was placed in 720-plastic containers (0.3 L volume; 4 cm diameter x 20 cm height) with 5 cm x 5 cm paper towel placed in the bottom of each container to allow water drainage and prevent the loss of soil. For each soil, 240 containers were planted at a rate of 4 seeds per container with one of the three following plant species: the invasive annual grass downy brome, the exotic perennial grass crested wheatgrass (*Agropyron cristatum*, cultivar Hycrest), and the

native perennial grass bottlebrush squirreltail (Rattlesnake germplasm). Certified perennial grass seed was obtained from a commercial source, while downy brome seed was collected from Box Elder County, Utah (Johnson Canyon, lat 41°53’32.61”N; long 112°12’55.53”W). Germination tests verified that seed viability was between 50 and 60%. Seeds were hand cleaned and selected for the experiment based on uniformity in size. Planting included placing four seeds of an individual species concentrically near the center of each container, covering with 5 mm of soil, and watering daily to initiate germination.

Four containers of each species were nested within each soil type within a rack, and individual container racks were randomly assigned to one of the six possible combinations of herbicide treatment (deionized water control, imazapic, and rimsulfuron) and application rate (70 or 105 g ai ha^{-1}). A rack from each of the six treatments was placed into a randomized complete block configuration on a greenhouse bench with 9 replicates. Prior to seedling emergence, herbicide treatments were applied in an enclosed spray chamber connected to an onboard control (E-410, Control Assemblies Co., Minneapolis, MN). Herbicide treatments were independently mixed and applied to replicate container racks. Spray was applied with an even-flat-fan nozzle (Teejet 8002, Spraying Systems Co., Wheaton, IL) calibrated to cover a 66 cm band at 76 cm s^{-1} at 105 kPa. The spray nozzle remained on a chain-driven path 40 cm above the soil surface. Numerous calibration trials were performed by spraying absorbent sheets of paper with deionized water and quickly weighing to determine application rate. The untreated control was applied in the same manner, except with deionized water. To avoid contamination between treatment applications, the sprayer

was rinsed with deionized water, and the spray chamber was thoroughly washed. After herbicide treatments were applied, racks were returned to the greenhouse, and plants were grown for an additional 27 d after treatment (DAT). Greenhouse temperature was maintained at 30°C during the day and 15°C at night with the aid of a greenhouse cooling system. No supplemental lighting was used, and the day length was roughly 16 h during the experiment. Each day individual containers were supplied with 15 mL of de-ionized water, which avoided the possibility of any water drainage, while adequately hydrating the entire soil. The 16 potential seedlings of each species within a container rack were considered an experimental unit.

Percentage seedling emergence was recorded throughout the experiment every other day. Shoot and roots were harvested at 27 DAT by emptying containers on a 2 mm screen, lightly washing soil from roots, and excising roots from shoots with a razor blade. Shoots and roots were combined into experimental units, and placed in a convective oven at 60°C for 48 h to determine dry mass. Percentage seedling mortality was calculated from the difference between maximum emergence and final seedling emergence.

Statistical analysis

This experiment was not repeated in time; however, herbicide solutions were independently mixed and applied at two rates. As an alternative, repeatability can be determined from the uniformity of herbicide impacts across herbicide rates, especially if differences are not statistically significant. Soil-property data from the salt desert and sagebrush sites were compared with Student t-tests. The randomized complete block design greenhouse study was analyzed as a factorial experiment with soil type,

herbicide treatment, herbicide rate, and grass species as main effects. Mean percentage seedling emergence is presented as opposed to cumulative percentages so it is clear to determine when seedling mortality was occurring. Final percentage seedling emergence at 27 DAT, percentage seedling mortality, and final dry mass of roots and shoots were analyzed with an ANOVA (general linear) model. Significant effects were further analyzed with Tukey's HSD mean separation procedure. Box-Cox transformations were performed on data as needed to improve normality and meet the assumptions of ANOVA. All analyses were performed with $P = 0.05$ using JMP 8 (SAS Institute, Cary, NC).

Results

The salt desert soil had significantly lower organic matter content, CEC, and percentages of clay and sand compared to the sagebrush soil (Table 2). In contrast, the salt desert soil had significantly greater soil pH, EC, and percentage of silt than the sagebrush soil.

Neither the main effect of herbicide rate nor any interactions with herbicide rate significantly influenced any of the experimental variables. Consequently, data for the two rates were combined and re-analyzed with reduced models (Table 3).

Seedling emergence was generally greater in the sagebrush soil than the salt desert soil, and crested wheatgrass and downy brome had similar emergence within a soil type (Table 3; Fig. 22). In contrast, seedling emergence of squirreltail was clearly lower than the other two grasses, but more so in the salt desert soil. While imazapic and rimsulfuron had similar effects on seedling emergence patterns relative to the

control in both soil types, seedling emergence in the rimsulfuron treatment was always significantly lower than the control, and the reduction by day 27 was 3-fold in the sagebrush soil and 1-fold in the salt desert soil (Table 3; Fig. 23). Likewise, imazapic and the control had similar effects on seedling emergence of all three grasses; however the reduction caused by rimsulfuron was significant for crested wheatgrass and downy brome, but not squirreltail (Table 3; Fig. 24).

Seedling mortality was contingent on how treatment and species interacted with shrubland soil types (Table 3). While herbicide treatments did not greatly influence mortality in the salt desert soil, both herbicide treatments significantly increased seedling mortality when applied to the sagebrush soil (Fig. 25A). Correspondingly, mortality was generally highest in the sagebrush soil, yet the difference between soil types was significant only for crested wheatgrass (Fig. 25B).

Treatment effects on shoot dry mass depended on significant interactions with both soil type and species (Table 3). Relative to the control, both herbicide treatments significantly reduced shoot dry mass in both soils; however, rimsulfuron reduced shoot dry mass significantly more than imazapic in the sagebrush soil type (Fig. 26A). Similarly, both herbicides significantly reduced shoot dry mass of crested wheatgrass and downy brome, but not squirreltail (Fig. 26B). Rimsulfuron reduced shoot dry mass more than imazapic for downy brome, but not for crested wheatgrass and squirreltail.

Soil type interacted with both treatment and species for root dry mass (Table 3). Both herbicides significantly reduced root dry mass relative to controls in both soils; however, imazapic showed greater reduction in the salt desert soil (Fig. 27A).

Root dry mass of squirreltail was also significantly lower than the other grasses only in the salt desert soil type (Fig. 27B).

Discussion

Reducing seed germination and emergence of invasive annual species greatly improves the success of seeding desirable seeded species (DiTomaso et al. 2000; Wisdom and Chambers 2009; Davies and Sheley *in press*). However, directly targeting these two critical processes with pre-emergence herbicides has been variable in semiarid rangeland soils (Monaco et al. 2005; Kyser et al. 2007; Morris et al. 2009), possibly because of differences in residual soil bioavailability. Our observation that both pre-emergence herbicides reduced seedling emergence and biomass production, yet increased mortality more so in sagebrush compared to salt desert soil, supports our hypothesis and clarifies how these two common Great Basin soils fundamentally differ in herbicide bioavailability. Consequently, we propose that physiochemical properties of these two soils may influence herbicide adsorption and subsequent leaching. Furthermore, because germination and emergence were clearly more impacted by rimsulfuron than imazapic, we present a detailed assessment of how two critical observations shed new light on the relative performance of these two promising herbicides, namely: 1) delayed injury in crested wheatgrass seedling emergence in the imazapic treatment, and 2) no reduction in downy brome seedling emergence in the imazapic treatment.

Because this was a controlled experiment, significantly greater herbicide impacts on seedling emergence, mortality, and growth in sagebrush soil relative to the

salt desert soil appears to be a consequence of the former soil having greater herbicide bioavailability. In general, soil adsorption, soil stability, and plant injury for pre-emergence herbicides strongly depend on soil colloidal properties; including organic matter content, clay content, and soil CEC (Morrica et al. 2000; Pusino et al. 2004; Monquero et al. 2008), which were notably higher in the sagebrush soil. Lesser impact of both herbicides on seedling shoot and root growth in the salt desert soil further emphasizes how lower herbicide adsorption relative to the sagebrush soil likely reduced bioavailability in our experiment. Bioavailability is also dependent on chemical hydrolysis and leaching. For example, rimsulfuron hydrolysis, resulting in contraction of the sulfonylurea bridge, takes place rapidly in distilled water (half-life = 2.2 d), is instantaneous in alkaline solutions above soil pH of 8, and accelerates at temperatures greater than 25°C (Schneiders et al. 1993; Dinelli et al. 1997; Martins and Mermoud 1999; Scrano et al. 1999). In addition to hydrolysis in aqueous solutions, pH also strongly influences adsorption and hydrolysis in soils, wherein adsorption of the sulfonylurea herbicide azimsulfuron was negatively correlated with pH (Pusino et al. 2004), and rimsulfuron hydrolysis was found to increase above pH of 7 in six Colorado soils (Vicari et al. 1996). Although less is known about imazapic bioavailability in soils, photolysis in aqueous solutions similarly increases with solution pH and temperature up to 40°C, and the rate of photolysis will plateau above pH of 5 (Harir et al. 2007). In soils, the adsorption of imazapic also decreases with increasing pH as the H^+ ion dissociates from the carboxylic group on the imidazolinone ring making the molecule predominantly negatively charged and more susceptible to leaching (Inoue et al. 2007, 2009). Furthermore, even in clay soils,

heavy simulated precipitation of 90 mm led to deep percolation of imazapic and poor weed control in superficial soil layers in sugarcane fields (Hernandez et al. 2001). In light of our experiment, lower herbicide adsorption and higher subsequent leaching in the salt desert soil thus appears to be a plausible mechanism responsible for the overall lower herbicide effect in our experiment, especially because ample water was applied to facilitate degradation and leaching within containers, soil pH was higher in the salt desert soil, and greenhouse temperatures exceeded 25°C each day.

The unique manner in which crested wheatgrass responded in our experiment provides a potential mechanism of how herbicide bioavailability varies between the two Great Basin soils we evaluated. Seedling emergence remained stable in the salt desert soil, but declined in both treatments after Day 11 in the sagebrush soil relative to the control, causing significant increases in mortality, primarily in crested wheatgrass (Figs. 23, 25A, and 24, respectively). This distinct pattern suggests that both herbicides may have experienced greater initial adsorption and subsequently lower leaching in the sagebrush soil, making crested wheatgrass more susceptible to injury. Greater initial adsorption in the sagebrush soil also likely provided more residual herbicide, prolonging the exposure of emerged crested wheatgrass seedlings. Lower adsorption, and subsequent leaching, in the coarse-loamy salt desert soil, would likewise have a diminished effect, by exposing seedlings to less herbicide, given its lower organic matter, lower CEC, and higher pH. Similar to our study, when rimsulfuron and two other sulfonlyurea herbicides were applied to bare soil with adequate adsorption potential, leaching was nearly undetectable, even under heavy irrigation in Canadian prairie soils (Cessna et al. 2010). Similarly, imazapic

experienced greater adsorption (lower dissipation time) in a clay soil than a sandy loam in Brazil (Ulbrich et al. 2005).

Our observation of no reduction in downy brome seedling emergence in the imazapic treatment was the most surprising result of our experiment. The question essentially becomes, why was downy brome emergence not reduced by imazapic even though this herbicide significantly reduced combined species mortality and drastically reduced shoot and root growth of this invasive annual grass? Although both herbicides were applied at the same active ingredient rates, it is possible that they fundamentally differ in plant uptake mechanisms and disruption of the acetolactate synthase (ALS) enzyme; however, neither of these factors were evaluated in our study (but see Stidham 1991: Tranel and Wright 2009). Another reason why imazapic did not reduce downy brome emergence may be the relative performance of pre-emergence herbicides, which typically differ in water solubility and extent of adsorption in soils (Singh et al. 1990; Barriuso et al. 1992). While direct comparisons of soil mobility and susceptibility to leaching between rimsulfuron and imazapic have not been made, our appraisal of independent studies is that leaching potential in soils is much greater for imazapic than rimsulfuron (Schneiders et al. 1993; Inoue et al. 2007, 2009; Cessna et al. 2010). These relative differences between imazapic and rimsulfuron are not only consistent with our interpretation of lower residual bioavailability in the salt desert soil, but also indicate the possibility that imazapic may have dissociated and leached within growth containers. Consequently, the combined effects of frequent watering and herbicide percolation may be responsible for 1) downy brome emergence not being significantly different between the control

and imazapic treatment, and 2) the delayed imazapic effect in crested wheatgrass. Furthermore, we suggest that only after roots elongated deeper into the soil were seedlings exposed to imazapic, and growth subsequently impaired. Finally, because imazapic did not reduce downy brome emergence and roots likely developed until they were exposed to imazapic, shoots were capable of achieving two-fold greater productivity than in the rimsulfuron treatment.

Lower herbicide injury to bottlebrush squirreltail than the highly responsive species–crested wheatgrass and downy brome–is not clearly explained by the responses we measured. It is likely that four-fold lower emergence of bottlebrush squirreltail in salt desert compared to sagebrush soil limited our ability to detect significant herbicide, or herbicide by species interactions. Although neither of the two herbicides we evaluated reduced any of the measured bottlebrush squirreltail variables, general patterns for mortality and shoot dry mass were similar to the responsive species. Consequently, we are reluctant to infer that bottlebrush squirreltail responds fundamentally different than the other grasses to these pre-emergence herbicides. Our position is supported by other studies that showed significant bottlebrush squirreltial injury from imazapic and other sulfonylurea herbicides (Monaco and Creech 2004; Sheley et al. 2007).

Implications

Principles linking ecological processes with invasive plant management are beginning to emerge for semiarid rangeland ecosystems (James et al. 2010). For example, failing to directly target invasive annual grass seed production, seed banks,

and seedling emergence can seriously hamper revegetation potential of a given site (Rafferty and Young 2002; Morris et al. 2009). Herein, we show the capacity of select pre-emergence herbicides to target seedling germination and emergence is strongly dependent on soil properties. Although this dependence is limited to the specific soils, herbicides, and seed sources we evaluated, our data suggest a number of implications to consider when using these herbicides to reduce invasive annual grass emergence and minimize non-target effects on revegetation species. First, our results suggest differences in residual herbicide bioavailability is a plausible mechanism for why initial control of annual grasses and injury to seeded revegetation species was found to be greater in sagebrush soils vs. salt desert soils (Morris et al. 2009). Given the broad variation in soil texture and organic matter within and between semiarid rangeland ecosystems, responses to pre-emergence herbicides may vary widely from site to site due to differences in soil herbicide bioavailability. These differences should be anticipated prior to selecting revegetation species and applying pre-emergence herbicides. Second, delayed plant injury and the potential differences we observed in herbicide adsorption and leaching, emphasize the importance of properly timing herbicide applications to avoid periods of high rainfall in semiarid rangelands. This may necessitate applying pre-emergence herbicides in the summer to insure high herbicide bioavailability when annual grasses begin to germinate and emerge with autumn precipitation, and to minimize injury to revegetation species, which increases as the time between application and seeding decreases (Sbatella et al. *in press*). Lastly, because herbicide efficacy depends on bioavailability in soils, we concur with previous suggestions that removing obstructive litter or vegetation from

the soil surface with management activities will greatly enhance soil adsorption and the effectiveness of pre-emergence herbicides (Monaco et al. 2005; Kyser et al. 2007; Davies 2010).

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Table 2. Results of physiochemical soil analysis of salt desert shrub and sagebrush ecological sites. Values are means (n = 15, except n = 5 for OM and CEC; ± 1 SE). All measures were significantly different between soils based on t-tests ($P < 0.05$).

Soil measure	Salt desert	Sagebrush
Organic matter (%)	1.80 (0.05)	3.78 (0.13)
Cation exchange capacity (cmol/kg)	15.88 (0.07)	19.62 (0.15)
pH	9.53 (0.01)	7.91 (0.01)
Electrical conductivity (dS/m)	0.352 (0.004)	0.257 (0.003)
Sand (%)	60.4 (0.3)	65.6 (0.3)
Silt (%)	30.6 (0.3)	23.3 (0.3)
Clay (%)	9.0 (0.1)	11.1 (0.1)

Table 3. Analysis of final seedling emergence, seedling mortality, and dry mass of shoots and roots from ANOVA. Significant effects with bolded *P*-values are emphasized in results.

		Final percentage seedling emergence		Percentage seedling mortality		Shoot dry mass		Root dry mass	
Effect	*df*	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Treatment (Trt)	2	43.21	<.0001	13.54	<.0001	48.72	<.0001	164.20	<.0001
Soil Type (ST)	1	62.71	<.0001	7.48	0.0067	28.07	<.0001	2.17	0.1422
Species (Spp)	2	46.35	<.0001	1.40	0.2496	19.40	<.0001	7.40	0.0008
Trt x ST	2	7.87	**0.0005**	6.66	**0.0015**	11.48	**<.0001**	31.36	**<.0001**
Trt x Spp	4	7.26	**<.0001**	1.74	0.1414	3.48	**0.0089**	1.27	0.2834
ST x Spp	2	6.43	**0.0019**	4.69	**0.0100**	1.55	0.2149	4.14	**0.0172**
Trt x ST x Spp	4	1.40	0.2335	2.27	0.0627	0.39	0.8178	1.16	0.3316

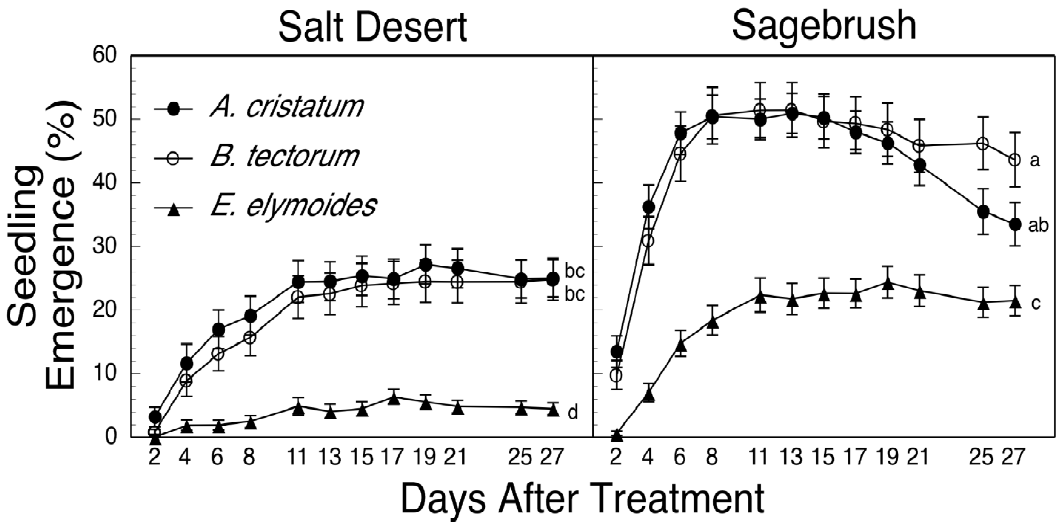

Figure 22. Mean (± 1 SE) percentage seedling emergence of three grass species grown in different shrubland soil types (combined herbicide treatments). Different lowercase letters indicate significant ($P < 0.05$) differences 27 days after pre-emergence herbicide application.

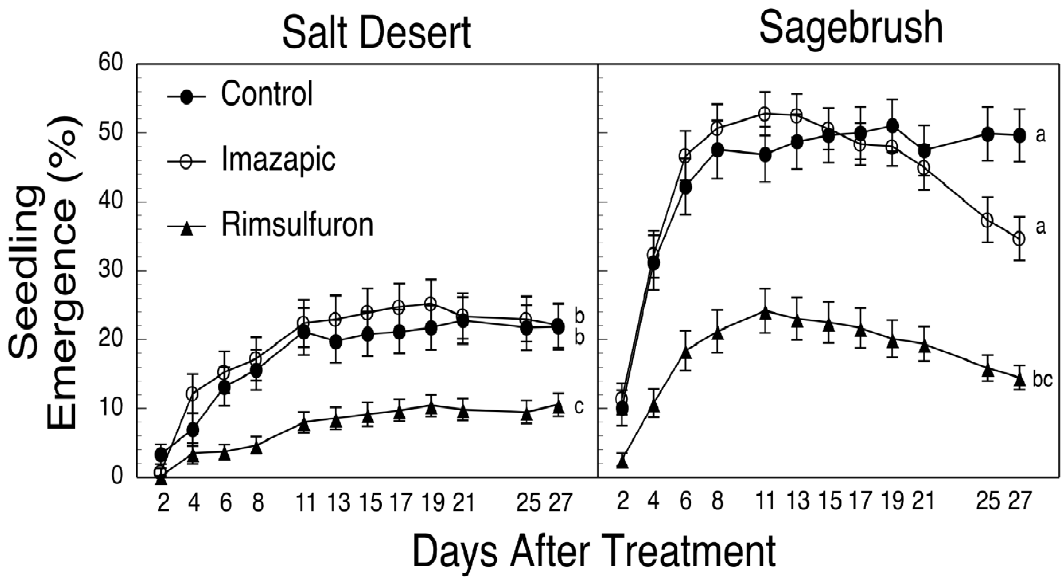

Figure 23. Mean (± 1 SE) percentage seedling emergence in different shrubland soil types following application of three herbicide treatments (combined grass species). Different lowercase letters indicate significant ($P < 0.05$) differences 27 days after pre-emergence herbicide application.

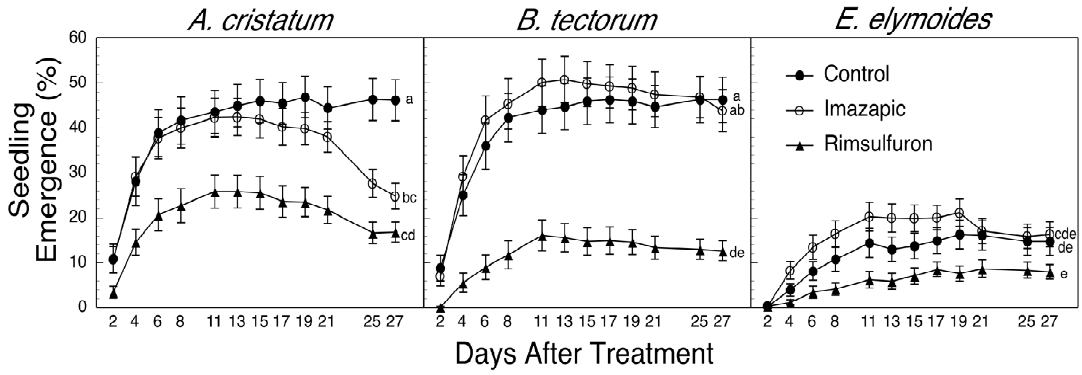

Figure 24. Mean (± 1 SE) percentage seedling emergence of three grass species following application of three herbicide treatments (combined shrubland soil types). Different lowercase letters indicate significant ($P < 0.05$) differences 27 days after pre-emergence herbicide application.

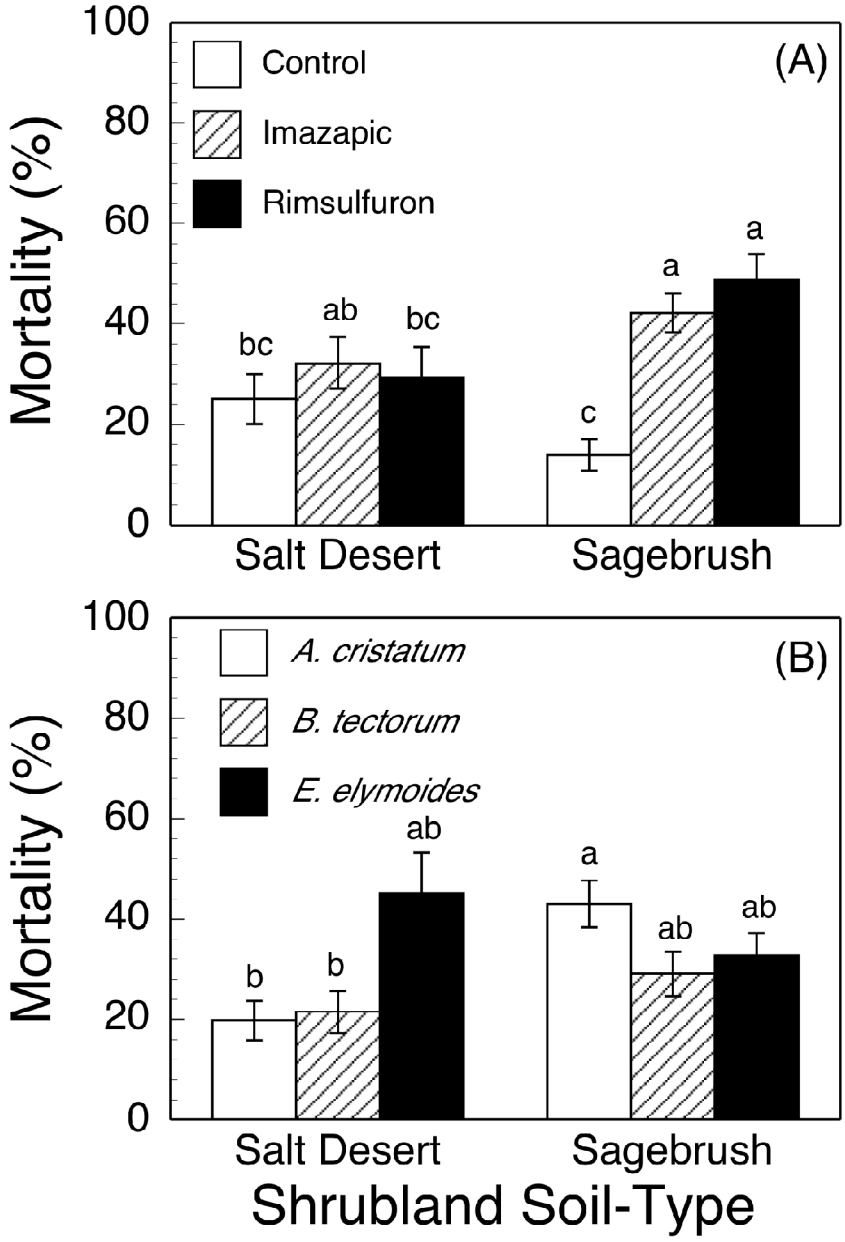

Figure 25. Mean (± 1 SE) percentage seedling mortality in different shrubland soil types following application of three herbicide treatments (A: combined grass species), and for three grass species (B: combined herbicide treatments). Different lowercase letters indicate significant ($P < 0.05$) differences 27 days after pre-emergence herbicide application.

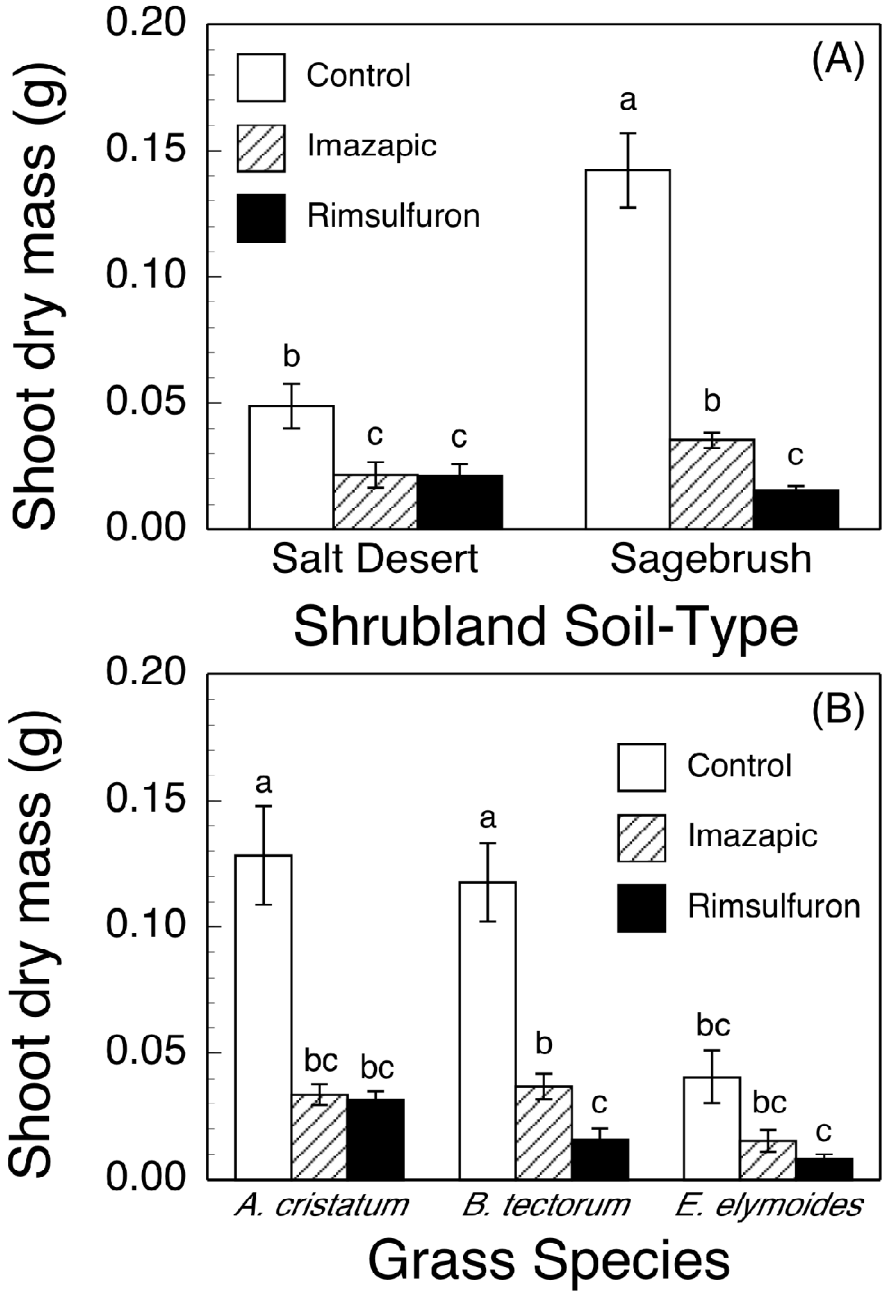

Figure 26. Mean (± 1 SE) shoot dry mass following application of three herbicide treatments to different shrubland soil types (A: combined grass species), and for three grass species (B: combined shrubland soil types). Different lowercase letters indicate significant ($P < 0.05$) differences 27 days after pre-emergence herbicide application.

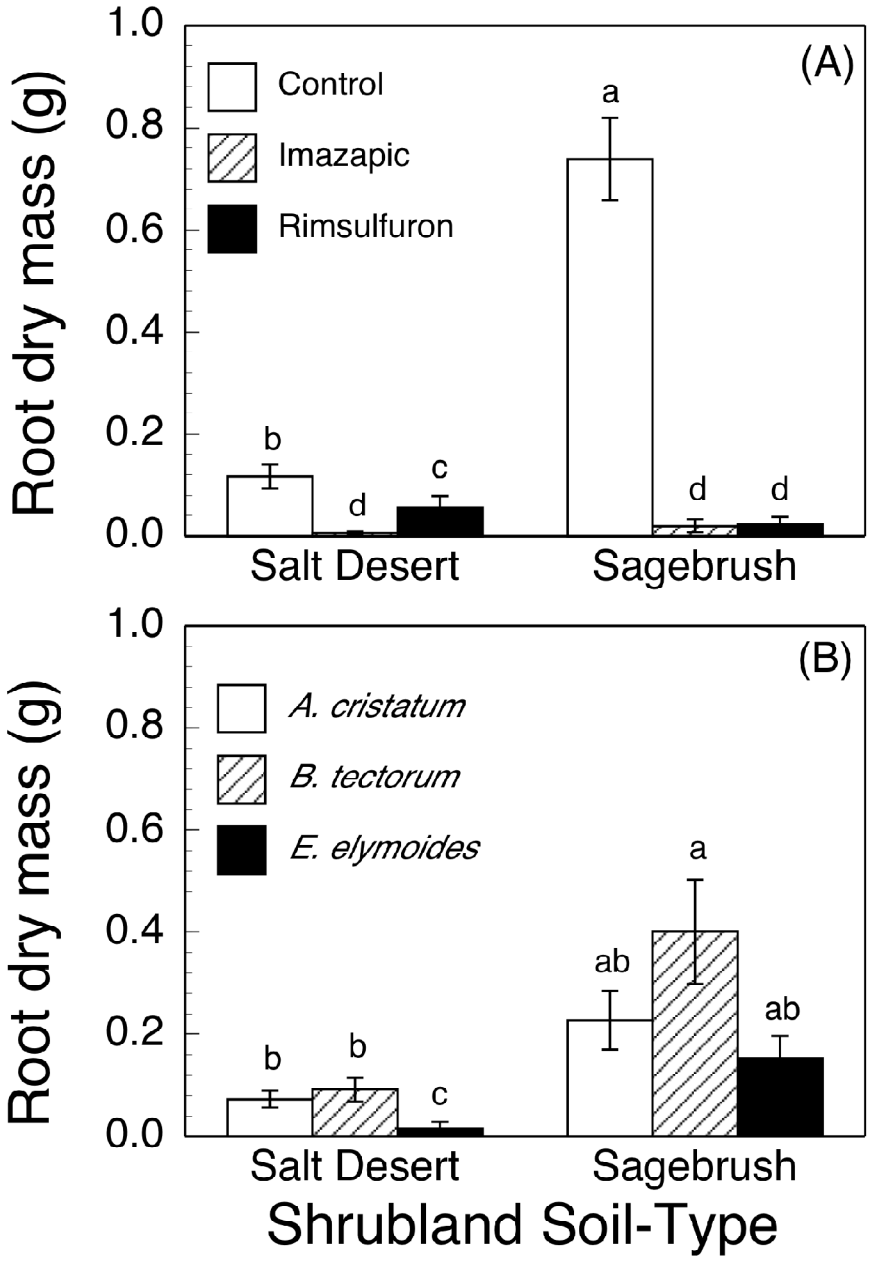

Figure 27. Mean (± 1 SE) root dry mass in different shrubland soil types following application of three herbicide treatments (A: combined grass species), and for three grass species (B: combined herbicide treatments). Different lowercase letters indicate significant ($P < 0.05$) differences 27 days after pre-emergence herbicide application.

CHAPTER 4

CONCLUSION

Ecological processes, including disturbance regimes, soil nutrient cycling, and successional pathways have been severely altered by the invasive annual grass downy brome (*Bromus tectorum* L.). As an ecosystem driver, downy brome also presents obstacles to land rehabilitation efforts, including restoring desirable species cover. Because damaged ecosystems may have crossed both abiotic and biotic thresholds, ecologically-based control strategies may assist with altering successional trajectories and restoring desirable plant species.

The results of my field study showcase the importance of the relationships between downy brome and soil nutrients on invaded salt desert shrublands and demonstrate that downy brome strongly influences water and nitrate availability. These results also identify that although burning and herbicide application both effectively reduce resource fluctuation and increase the availability of soil water and nitrate, burning was by far the most overall effective treatment to reduce downy brome abundance, interannual fluctuation, and prepare the soil surface for seeding desirable species. In addition, my results imply that the only real strategy to avoid reinvasion and maintain site stability by reducing resource fluctuation is to establish perennial species. Resident species at my sites, and most likely others dominated by downy brome within the Great Basin are incapable of entirely filling the void when downy brome is controlled. Thus, successful establishment of perennial species should occur during the time of weakened downy brome and stabilized resource

availability, so that over time perennial species can gain dominance and begin to control plant-soil dynamics.

Although the results of these studies showcase the importance of process-based annual grass management, they also bring up new questions for ecological research on severely degraded downy brome dominated shrublands. For example, although we suggest that the above ground botanical composition drives the variability of belowground resources, we have not identified at which point thresholds become crossed and repairing processes become virtually impossible without the assistance of seeding. It is possible that belowground variables are the determining factor that determines ecological thresholds as well as the degree to which restoration strategies need to be implemented. For example, if soil factors are found to be severely degraded, then seeding may be inevitable, whereas if soil properties are still functioning then it may be possible to direct succession of the aboveground community with control treatments alone. However, testing this in the field is critical to understanding the degree to which soil properties influence these successional pathways and threshold values. In addition to identifying how belowground variability affects succession, characterizing the response of how seeded species germinate and emerge based upon the variability of soil resources on degraded systems could also provide important information on understanding species success as well as the revegetation requirements when seeding. Following the effects of the control treatments on both seeded species establishment and resident species abundance would likely help to predict the best management practices for these ecosystems.

The greenhouse study provided critical information regarding herbicide mechanisms in two shrubland soil types and on three different grass species that are commonly found throughout the Great Basin. For example, the greenhouse study showcased that the capacity of select pre-emergence herbicides to target seedling germination and emergence is strongly dependent on soil properties. Although this dependence is limited to the specific soils, herbicides, and seed sources I evaluated, these data suggest a number of implications to consider when using these herbicides to reduce invasive annual grass emergence and minimize non-target effects on revegetation species. First, these results suggest differences in residual herbicide bioavailability is a plausible mechanism for why initial control of annual grasses and injury to seeded revegetation species was found to be greater in sagebrush soils vs. salt desert soils. Given the broad variation in soil texture and organic matter within and between semiarid rangeland ecosystems, responses to pre-emergence herbicides may vary widely from site to site due to differences in soil herbicide bioavailability. In addition, because herbicide efficacy depends on bioavailability in soils, removing obstructive litter or vegetation from the soil surface with management activities will greatly enhance soil adsorption and the effectiveness of pre-emergence herbicides.

Although these data presented from the greenhouse study provide crucial information for the management of downy brome dominated shrublands with pre-emergence herbicides, there may be ways in which the information that we presented could be improved. For example, although, the greenhouse study suggested possible mechanisms for herbicide response to target and non-target species in the two shrubland soil types, it is crucial that it be field tested before coming to an absolute

conclusion. Therefore, testing the effects of these herbicide treatments on soils and species in the field for several consecutive years is also important to understanding residual effects of herbicides in these Great Basin soils as well as to predict the most successful treatment options for these severely degraded shrublands. Collectively, these studies showcase the importance of managing processes to reduce the effects of downy brome on highly invaded salt desert shurublands, however, in order to continue to see a positive trend toward annual grass reduction and perennial grass dominance, management on these systems should be ongoing and continuous. With the continuation of developing better management practices for restoration success on these systems the continued dominance and spread of downy brome may be reduced and stability may again be restored on these degraded shrublands.